

FIRE HISTORY

FIRE HISTORY AND EFFECTS ON VEGETATION IN THREE BIOGEOCLIMATIC ZONES OF BRITISH COLUMBIA

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Abstract—The different fire regimes present in the province of British Columbia are well-illustrated by the Coastal Western Hemlock, Boreal White and Black Spruce, and Ponderosa Pine Biogeoclimatic Zones. Fires are variable in type, intensity, severity, effects, size, and interval. In the first two biogeoclimatic zones, stand replacement and/or partial stand replacement fires occur. Surface fires that maintain open forests with grassy understories are the historic norm in the Ponderosa Pine Zone.

Fire histories and fire effects have been determined for all three zones. In the Coastal Western Hemlock Zone the emphasis has been on fire history, stand establishment, and prescribed burning. Ecosystem-specific guides describing the type of fire suitable for silvicultural site preparation are widely available. Post-fire vegetation successional pathways have been developed for the Boreal White and Black Spruce Zone and are used to predict probable fire outcomes.

In recent times, the adverse implications of fire exclusion have been recognized in ecosystems such as those found in the Ponderosa Pine Zone. The reintroduction of fire through prescribed burning serves to address the problems and meet several resource management objectives.

INTRODUCTION

British Columbia is a large and ecologically diverse province. It covers a total area of 94,900,000 ha, of which 52,200,000 ha are forested (Farley 1979). The vegetation has been classified into fourteen biogeoclimatic zones which range from, but are not limited to, coastal rainforests, southern grasslands, northern boreal forests, and alpine tundra (Pojar 1983; Pojar and others 1987).

The fire history and fire ecology of these biogeoclimatic zones have been studied to varying degrees, depending on location, the management agency, and context.

OBJECTIVES

The objective of this paper is to describe the fire history, and general fire ecology, of three biogeoclimatic zones. For several of the fourteen zones little information exists and in others the focus has often been on just one subject area, such as prescribed fire effects. By choosing three zones to examine, a range of conditions within the province can be illustrated.

An historical perspective is provided since much of the older, as well as some of the more recent, fire history work done in the province has received little exposure to date.

COASTAL WESTERN HEMLOCK ZONE

This zone occupies low to middle elevations, mostly west of the coastal mountains, along the entire B.C. coast, on Vancouver Island and the Queen Charlotte Islands (fig. 1). It

is the wettest zone and has cool summers and mild winters. Mean annual precipitation is from 1,500 to 4,400 mm (Pojar and Klinka 1983).

The major tree species present are western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*). Douglas-fir (*Pseudotsuga menziesii*) is present in the drier subzones; amabilis fir (*Abies amabilis*) and yellow-cedar (*Chamaecyparis nootkatensis*) are common only in the wetter subzones. Present, but restricted to certain habitats, are grand fir (*Abies grandis*), western white pine (*Pinus monticola*), Sitka spruce (*Picea sitchensis*), bigleaf maple (*Acer macrophyllum*), red alder (*Alnus rubra*), black cottonwood (*Populus balsamifera* ssp. *trichocarpa*), and shore pine (*Pinus contorta* var. *contorta*).

Fire History

Evidence of fire primarily takes the form of charcoal layers in the soil, fire-scarred trees (primarily Douglas-fir), charred bark, and even-aged stands of shade-intolerant species. The fire regime consists of long interval severe crown and surface fires which result in total stand replacement. Lower severity surface and crown fires with partial stand replacement are also common, often within the larger more severe burns.

Historically, large areas burned when lightning-caused fires occurred during extended regional summer droughts. Physiography plays a role in fire history as well, with differing fire incidence being a function of elevation, topography, and aspect (Schmidt 1960).

The fire history of the Coastal Western Hemlock Zone in British Columbia was first studied in the early part of this

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century. The situation is complicated by more than 1.50 years of human disturbance. Removal of the original forests and their replacement by second-growth plantations, in combination with wildfires and prescribed burns, has made the determination of historical fire frequencies difficult or impossible in many localities.

Rigg and Richardson (1938) noted the presence of charred remains in many bogs in northwest Washington and southwestern British Columbia but did not indicate how long fire had been a factor in the regional landscape. In lake sediments from the adjacent western hemlock zone of Washington state, Cwynar (1987) dated Douglas-fir and western hemlock pollen mixed with charcoal fragments to 11,000 years before present. Climatic change has occurred since then, and with it the fire regime and relative abundance of the two conifer species.

Fire intervals likely range from 150 (Martin and others 1976) to 350 years or more but may not be truly cyclic (Agee 1981). Fahnestock and Agee (1983) estimated the fire cycle for western hemlock forests of western Washington to be 598 years. The value for western redcedar forests was 3,116 years but the authors considered that figure to be unexpectedly long. Agee (1990) calculated a fire cycle of 400 years for the cedar/spruce/hemlock type in Oregon.

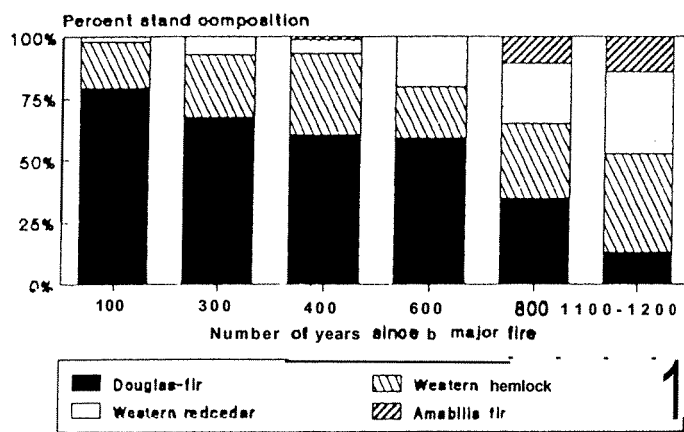
Dendrochronology has revealed fires as early as 670 A.D. in Douglas-fir forests on northern Vancouver Island (Schmidt 1970). The even-aged character of these stands, coupled with charcoal in the soil and charred bark on veteran trees, denoted a fire disturbance history. A second disturbance by fire may result in a stand with two major age classes. Significant fire years on the British Columbia coast are indicated for approximately 1100, 1210, 1410, 1560, 1610, 1660, 1740, and 1820 (Schmidt 1970).

Howe (1915) found that Douglas-fir forests in this zone generally originate after fire. Stand establishment dates suggest fires occurred in 1454, 1489, 1558, 1814, and 1844. Scars on large old trees recorded fires in 1598, 1684, and 1844.

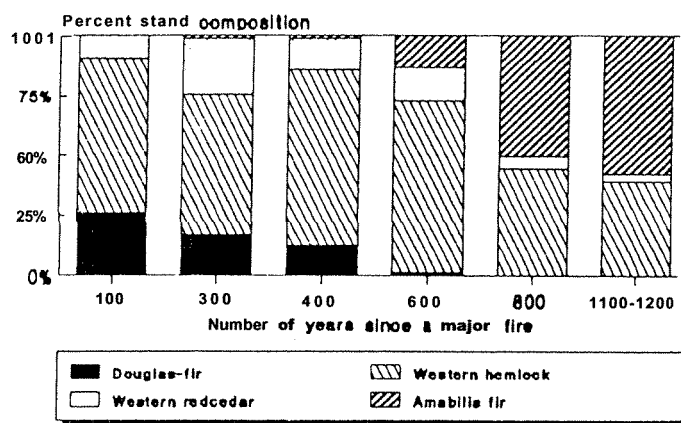
Eis (1962) also considered the oldest tree layer to be indicative of a fire year, with younger and lower layers recording subsequent and less severe disturbances. Based on stand ages, fires are indicated for the lower mainland coast around 1540, 1550, 1660, 1690, 1770, 1790, 1840, 1860, and 1890.

Correlations of fire dates within and between the data for different localities in Schmidt (1970), Howe (1915), and Eis (1962) indicate more prominent fire years for the lower British Columbia coast as 1489, 1558, 1660, 1684, 1690, 1820, and 1890. Mathewes (1973) found a charcoal-rich lake sediment layer which might very well coincide with a

FOREST SUCCESSION ON VANCOUVER ISLAND Large trees



Intermediate trees



Advance regeneration

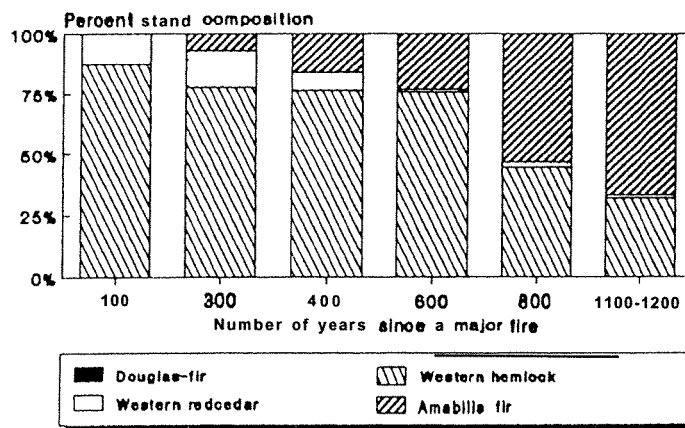


Figure 1. Location of biogeoclimatic zones.

significant (800,000 ha) regional fire event in the mid-1600's described by Schmidt (1957) and/or a local fire dated to around 1660 by Eis (1962).

On the north coast, other disturbance agents such as wind and landslides may be more important than fire. Harris and Farr (1974) noted that while there are significant areas of even-aged stands on the Alaska panhandle which apparently owe their origin to fire, the bulk of the forests there are uneven-aged. Age class structure suggests that extensive fires burned in 1664, 1734, and between 1804 and 1824. Since 1900 few fires have burned more than 40 ha.

Fire Effects and Succession

At a large scale, Schmidt (1960) felt the lower incidence of forest fires on the north coast was responsible for limiting the range of Douglas-fir. Western redcedar continues north for 480 km beyond the range of Douglas-fir, and western hemlock for 1,100 km. Douglas-fir is capable of growing outside its range but this has been prevented as, without fire, the species cannot colonize new habitat.

On a site basis, post-fire vegetation succession in the Coastal Western Hemlock Zone has been of interest for quite some time. A pioneering study concluded that repeated burning was destroying the seed trees and young growth (Howe 1915). On one-half of the land examined, which had been logged and burned over between 1884 and 1914, the reproduction of new forests was considered inadequate. This was attributed to an increase in the frequency of widespread fires from every 86 years for the period from 1554 to 1814, to 27 years for the period from 1814 to 1894, to 5 years between 1894 and 1914 (Howe 1915).

Howe (1915) observed that most young Douglas-fir forests were establishing on areas which had been burned or logged and burned. He found Douglas-fir established best on moderately-burned areas and likely required fire to clear away the slash and lesser vegetation. Western hemlock reproduction was encouraged by light surface fires beneath Douglas-fir stands as the moss layer, which usually develops after fire, conserves moisture and is an ideal medium for seedling germination (Howe 1915).

When established together, western hemlock seedlings may initially outnumber those of Douglas-fir, but the latter species is more robust and has the advantage on exposed post-fire sites with thin duff layers (Agee 1990). Understory vegetation primarily consists of species which sprout from underground rhizomes or from the bud collar (Agee 1981).

By 20 years post-fire most of the snags have fallen and succession has led to a highly diverse shrub stage which supports much wildlife (Agee 1981 and 1990). Shrub and herb cover later decline as the tree canopy develops and closes. Small openings in the canopy resulting from

windthrow, snowbreak, insect kill, or disease will be occupied by the more shade-tolerant conifer species, with Douglas-fir limited to the dominant trees which established soon after the fire. If western hemlock did not become established with Douglas-fir during the initial post-fire succession phase, and form part of the main canopy, it may appear after 50 or 100 years have passed (Franklin and Dymess 1973).

After several centuries Douglas-fir density continues to decrease, while the lower crown classes become occupied by western hemlock, western redcedar, and amabilis fir (Agee 1981; Munger 1940; Schmidt 1970; Spies and Franklin 1988). Understory regeneration of western hemlock and amabilis fir may be limited by a dense western hemlock canopy until it starts to break up after 300 to 400 years (Stewart 1986). Decline of the Douglas-fir component may begin at 500 years, or be delayed until after 1,000 (Franklin and Spies 1984).

Munger (1940) and Schmidt (1957) described the later stages of development of these stands when Douglas-fir gives way to the shade-tolerant species. Schmidt's data from 142 plots on Vancouver Island showed initial post-fire recolonization by Douglas-fir, western hemlock, and western redcedar (fig. 2). Amabilis fir is less capable of invading the burned site and depends upon the offspring of its initial colonists to extend itself. As time since fire increases, the species composition shifts away from Douglas-fir and western redcedar to western hemlock and amabilis fir. The long-term absence of fire results in the loss of Douglas-fir.

It has been known for some time that most of the Douglas-fir forests in the Coastal Western Hemlock Zone are seral to the climax western hemlock and western redcedar (Benedict 1915; Eis 1962; Franklin and others 1981; Howe 1915; Judd 1915; Munger 1940; Wright and Bailey 1982) and long believed that post-fire Douglas-fir forests are generally even-aged (Franklin and Waring 1979; Judd 1915; Munger 1940).

Indeed, Munger's data showed the Douglas-firs on a 65 ha plot to be nearly all within 25 years of 590 years of age. The western hemlocks of that stand, by contrast, ranged in age from 130 to 525 years. Recent work has found that the range in age of the dominant old-growth Douglas-fir trees may surpass 200 years, indicating a lengthy site reoccupation period (Franklin and Waring 1979; Franklin and others 1979). This may be due to a lack of seed source (necessitating gradual recolonization), vegetative competition (delaying tree establishment), or multiple disturbances (partial reburns removing portions of the first stand) (Franklin and Waring 1979).

Resource Management Implications

Prescribed burning to remove logging slash and produce conditions amenable to the establishment of Douglas-fir, the preferred species, was considered a necessity (Howe 1915) and has been carried out since the early part of this century.

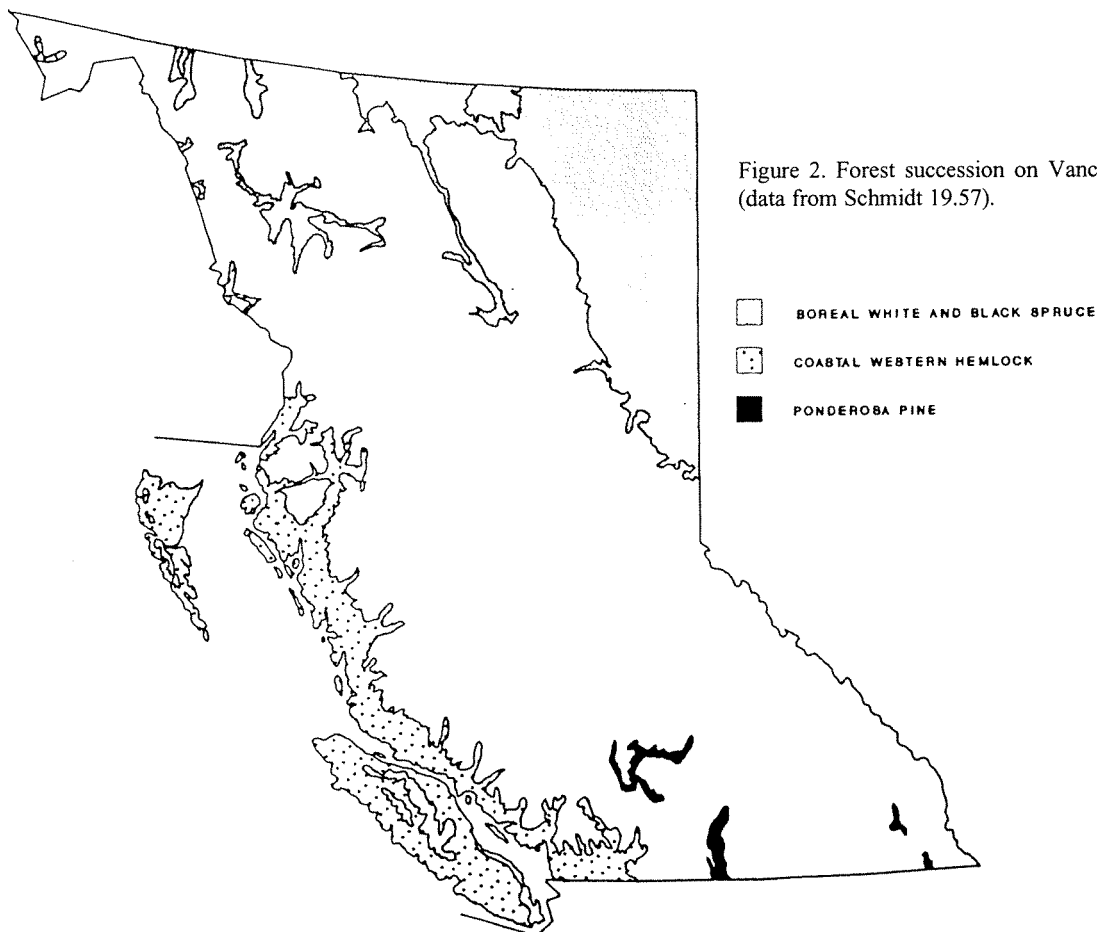


Figure 2. Forest succession on Vancouver Island (data from Schmidt 19.57).

Although compulsory slash disposal was not imposed on logging operators when the Forest Branch was created in 1911, such actions were encouraged. Without prescribed burning after harvesting, it was expected that western hemlock **would** predominate (Benedict 1915). In northern parts of the zone, where soil conditions were different, slash disposal by burning was not recommended.

Fire effects in the Coastal Western Hemlock Zone have generally been studied in the context of using prescribed fire for site preparation. Considerable research has been carried out and continues by provincial and federal government agencies, local universities, and forest companies (Beese 1986; Cameron 1988; Peterson 1989).

Ecosystem-specific guides describe the proper use of prescribed fire (Haeussler and others 1984; Klinka and others 1984). Recommendations are made as to whether prescribed fire should be applied to a site and if so, what particular fire effects are suitable.

Concern is growing over the need to preserve islands of old growth timber generally comprised of western hemlock, western redcedar, Douglas-fir and sometimes Sitka spruce (Spies and Franklin 1988). With long interval fires which can grow to significant size, careful planning will be required to preserve these old-growth islands. The need to consider the role of natural fire in their life cycle is obvious.

BOREAL WHITE AND BLACK SPRUCE ZONE

The Boreal White and Black Spruce Zone occupies the low to middle elevations of the northern portion of the province, primarily in the northeast corner (Annas 1983). It has a northern continental climate with long, very cold winters and therefore a short growing season. Discontinuous permafrost exists in some locales.

The Boreal White and Black Spruce Zone is floristically very diverse. Major tree species include white spruce (*Picea glauca*), black spruce (*Picea mariana*), lodgepole pine (*Pinus contorta* var. *latifolia*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), Alaska paper birch (*Betula neoalaskana*), tamarack (*Larix laricina*), and subalpine fir (*Abies lasiocarpa*). Balsam poplar (*Populus balsamifera* spp. *balsamifera*) and white spruce occupy alluvial floodplains.

Fire History

Physical evidence of fire in the boreal forest is found in the form of charcoal deposits in the soil profile; fire-scarred trees and charred snags; as well as in the mosaic character of the forest stands, their age structure, and the morphological and reproductive characteristics of the plant species present (Rowe and Scotter 1973). The forest mosaic may take on the appearance of a patchwork quilt, with each patch being sharply differentiated by abrupt changes in tree species

composition and crown heights. Within each component the stand structure and composition may be remarkably uniform (Dix and Swan 1971).

The fire regime consists of short to long interval crown fires and severe surface fires in combination. Stand replacement fires are the norm and surface fires alone are rare, occurring along the edges of crown fires where fire behavior was moderated. Ground fires can be persistent in deep organic soils.

Hazardous fire weather conditions are encouraged by lengthy summer days which result in long diurnal drying periods as well as by extended periods of low precipitation and humidity. In northern British Columbia very large lightning-caused fires have occurred decadal and reached 180,000 ha. Man-caused fires have sometimes surpassed this size during the past 50 years.

Heinselman (1981) summarized fire regimes for the boreal forest. Presettlement fire cycles ranged from 50 to 200 years for types shared by the Boreal White and Black Spruce Zone of northern British Columbia. Fire cycles there differ between forest types, but likely average 140 years.

Since most of the landscape in this zone is subject to fire, stand age class distribution data have been used to model fire cycles and the effects of fire suppression. For northwestern and northeastern British Columbia, fire cycles were 125 and 202 years respectively (Smith 1981). However, a regional fire cycle is a composite, with the components having their own shorter or longer cycles as a function of site type (Rowe 1983).

Although much evidence exists for aboriginal burning and an increased fire frequency due to the presence of European man in the boreal forest (Lutz 1959), specific references to northern British Columbia are rare. House (1909) told of a hunting expedition in northwestern British Columbia during which his native guide set several grass fires in order to approach a herd of caribou under the cover of smoke.

Lewis's (1982) native informants in northern Alberta described the use of prescribed fire for creating and maintaining meadows, manipulating riparian vegetation, clearing campsites and trails, removing windfalls, and creating firewood. It is likely that such practices were carried out in the boreal forest of neighboring British Columbia, influencing the fire regime there as well.

Lutz (1959) documented fires in the boreal forest caused by European man's escaped campfires as well as his deliberate firing of the forest in order to create supplies of dry fuelwood, signal other parties, drive moose, and promote the growth of forage for domestic stock. Fire was also used to remove local forest cover, thus thawing the permafrost and permitting excavation for minerals (Dawson 1888).

Fire Effects and Succession

The natural role of fire in the boreal forest of North America has been described in detail (Foote 1983; Kayll 1968; Kelsall and others 1977; Lutz 1955; Rowe 1983; Rowe and Scotter 1973; Viereck and Schandelmeier 1980). With stand-replacing crown fires and tree species which are fire sensitive and usually killed by fire, forest regeneration depends on "on-site" or "off-site" adaptations.

On-site adaptations to fire include cone serotiny (lodgepole pine), semi-serotiny (black spruce), root suckering (trembling aspen), and root collar sprouting (paper birches). Species such as white spruce, tamarack, and subalpine fir require live survivors off-site but near enough to provide seed to the burned area. The hardwoods produce prolific amounts of light seed which, if carried by the wind to the burned site, may result in a post-fire hardwood component as well.

Lesser vegetation also possess post-fire reproductive strategies, such as sprouting from roots, rhizomes, and stems, or the production of many light wind-disseminated seeds (Rowe 1983). Some, such as high bush cranberry (*Viburnum edule*) and pink corydalis (*Corydalis sempervirens*) have seeds that germinate following stimulation by fire (Viereck and Schandelmeier 1980).

Natural regeneration of tree species after fires in the Boreal White and Black Spruce Zone is quite prompt; many forest stands show an age range of only 10 to 15 years, sometimes up to 20. A wave of tree establishment often takes place in the first 5 to 7 years. However, where initial restocking levels are low and seed source, seedbed, and vegetative competition conditions continue to be favorable, recruitment may continue for several decades (Parminster 1983).

Post-fire changes in floristic composition may be minor, with succession becoming an exercise in changing structure and species dominance. For instance, black spruce - sphagnum moss and black spruce - lodgepole pine types generally exhibit little change in composition as time since fire increases. Even though identifiable stages exist (Foote 1983), vegetation cycling by fire rather than orderly replacement of species through succession is common (Methven and others 1975; Viereck 1983).

In other situations, the proportion of the post-fire stand made up by early successional species, such as trembling aspen, the paper birches, and lodgepole pine, may increase over the pre-fire values for those species. Indeed, they may not have been present at all. Other species, such as white spruce, black spruce, and subalpine fir, will be less represented on a proportional basis until later in the life of the stand.

Although trembling aspen and lodgepole pine overtop white spruce during most of the stand's lifetime, the latter species survives and eventually replaces the former in the absence of

fire. In most cases all three species become established simultaneously post-fire (Parminter 1983). A similar situation holds for lodgepole pine and black spruce, and lodgepole pine and subalpine fir mixes. Notably, if fire returns before the more shade-tolerant species (the spruces and subalpine fir) are sexually mature, the more fire-adapted early successional species (trembling aspen, paper birches, and lodgepole pine) will have the upper hand and dominate the post-fire site.

Resource Management Implications

Fire suppression costs in the Boreal White and Black Spruce Zone can be high, the annual area burned large, and the economic value of much of the timber resource relatively low. Therefore, fire effects and post-fire vegetation response are important when making decisions on appropriate wildfire suppression response (as well as in planning for prescribed burning).

Post-fire vegetation development depends on many factors such as the type of pre-fire vegetation present and its state of development; the season of fire occurrence; fire behavior and intensity; the depth of burn; fire size; the nature of the off-site vegetation; physical site characteristics; and post-fire environmental conditions. In spite of all of these variables, the most likely course of post-fire succession can be anticipated.

Post-fire vegetation succession models act as predictive tools to aid in resource management decision-making. After 17 cover types in the Boreal White and Black Spruce Zone were delineated following the approach of Hansen and others (1973), a modification of Kessell and Fischer's (1981) methodology was used to show the multiple pathways of post-fire succession. The possible post-fire outcomes, and the further development of the cover types with and without fire, have been detailed (Parminter 1983).

Considerable prescribed burning is carried out to enhance domestic range and wildlife habitat (primarily for large ungulates). Conversion of coniferous to mixedwood stands or of mixedwood to shrub- and herb-dominated types occurs as prescribed burning shortens the fire frequency.

PONDEROSA PINE ZONE

This zone is found at lower elevations in some of the main valleys of the southern third of the central interior. It extends south into the Pacific Northwest states.

Climatically it is the driest, and in summer the warmest, biogeoclimatic zone in the province (Mitchell and Erickson 1983). It is classed as semi-arid continental. The summers are warm and the mean annual precipitation ranges from 200 to 300 mm. Moisture deficits occur during the growing season.

Ponderosa pine (*Pinus ponderosa*) is the predominant tree species, and often forms open park-like stands with an understory of bluebunch wheatgrass (*Agropyron spicatum*). Douglas-fir and trembling aspen occur on moister sites, and western larch (*Larix occidentalis*) is rarer. Grasslands are mixed with the forest cover throughout the zone.

Fire History

Evidence of fire is found as charcoal layers in the soil, charred bark, and fire-scarred trees (primarily ponderosa pine and Douglas-fir). The fire regime most often consists of frequent light surface fires and, rarely, long interval crown fires. The role of fire is to maintain the stand, keeping the understory relatively open and the ground free of excessive woody fuel buildup (Agee 1990). The rarer crown fires in this type open up gaps within the stand which then fill in with a new age class of ponderosa pines.

Charcoal deposited in lake sediments from local and regional grassland and forest fires indicated a fire history going back 300 years or more in the southern part of the Ponderosa Pine Zone (Cawker 1983). Many fires have been lightning-caused. A proportion can be attributed to aboriginal prescribed burning, which Barrett and Arno (1982) and Gruell (1985) found to have increased fire frequency in ponderosa pine habitats of the interior western states.

Fire history studies in North America have revealed fire frequencies of about 6 to 15 years for the types of ponderosa pine stands found in British Columbia (Wright 1978; Wright and Bailey 1982). One of the earliest local investigations was that of Melrose (1923). In the southeastern portion of the province he dated 13 fire events between 1729 and 1908, for a fire frequency of 13.7 years.

Dorey (1979), working just above the Montana border, constructed a fire chronology based on 14 fire-scarred trees which indicated a history of surface fires between 1813 and 1940. The fire frequency works out to 6.3 years overall.

Cartwright's (1983) data show a fire frequency of 9 years for a mixed ponderosa pine - Douglas-fir forest near Kamloops, British Columbia. Low (1988) found values of 7.2 and 10.5 years for two areas in the same vicinity.

Fire Effects and Succession

Windfall, insect attacks, mortality, and frequent fire have historically maintained open ponderosa pine and mixed ponderosa pine - Douglas-fir stands (Wright 1978). Tree seedlings established after fire begin the development of an even-aged group. An uneven-aged forest results from this pattern.

Under a natural regime most of the understory grasses, forbs, and shrubs are maintained and enhanced by fire. Low severity fires favor resprouting, while germination from seed is favored after high severity fires (Saveland and Bunting 1988). However, mortality of fire-sensitive understory species, as well as conifers, does take place.

Fuel removal by grazing of domestic stock and fire suppression has significantly affected fire frequencies, either lengthening them substantially or removing the influence of fire altogether. Dorey (1979) found the fire frequency to have been 5.9 years prior to, and 9.6 years after 1911. No fires took place since 1940. Low (1988) found an area with a fire frequency of 10.5 years between 1672 and 1900 which had not experienced fire since 1901. Another with a fire frequency of 7.2 years between 1774 and 1933 had not had a fire since 1934.

Early accounts of the ponderosa pine forests described them as being fairly open and interspersed with large areas of grassland. Crown fires seldom occurred in these types (Whitford and Craig 1918). With fire exclusion, such stands become dense, many younger trees establish in the understory, and tree growth stagnates (Amo 1988). Total fuel loading becomes higher and the amount of ladder fuels increases dramatically, increasing the possibility of crown fires (Steele and others 1986). Douglas-fir often invades the lower canopy and becomes predominant, where before it had been absent or minor (Amo 1988; Dorey 1979). Understory vegetation becomes depleted due to the denser tree canopy.

Resource Management Implications

Historical sentiment against underburning these ponderosa pine forests related to the death of young seedlings, loss of timber production, scarring of trees, and depletion of soil nutrients (Melrose 1923). The opinion of the Forest Branch was that a continued role for surface fires in these stands would be an economic misfortune (Forest Branch 1923).

The ecological consequences of the exclusion of fire from these stands have been recognized in the past two decades. Prescribed burning is now carried out in many ponderosa pine and mixed ponderosa pine - Douglas-fir forests to maintain and enhance domestic range and wildlife habitat. Other reasons include fuels reduction (especially in the urban/wildland interface zone) and visual resource management. Prescribed fire may be combined with mechanical treatments, such as spacing, thinning, pruning, or selection logging.

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ANTHROPOGENIC FIRE AND TROPICAL DEFORESTATION: A LITERATURE PERSPECTIVE

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Abstract—Anthropogenic fire is an important agent of tropical destruction. Fire has been the primary tool of rural and technologically primitive people for managing and manipulating their natural environment. For more than a century observers and researchers have recorded and documented the process of deforestation by fire throughout the tropics. Using the cumulative written work of these investigators, we describe how human-caused fire in the tropics has contributed to deforestation. Human use of fire cannot be eliminated, nor is its elimination necessarily desirable; however, it must be managed. Education of fire users must form the core of any fire management program. Until an effective fire management policy can be implemented, anthropogenic fire will continue to contribute to tropical deforestation.

INTRODUCTION

Fire in nature is an awesome force. In human hands it has become our most powerful tool for altering the face of the earth (Sauer 19.58). Today, as it has been since mankind first learned to use it, fire is the primary tool of rural and technologically primitive people for manipulating and managing their natural environment (Stewart 1956).

Unfortunately, fire has become one of the most important agents in the worldwide destruction of tropical forests, and 98 percent of tropical fires are anthropogenic, started by some intentional or unintentional human action (Batchelder 1967). Anthropogenic fire has been identified as the most serious threat to Venezuela's forests (Budowski 1951; Camero-Zamorra 1952). In India human-caused fire has been responsible for the loss of much of the subcontinent's forests (Troup 1926). On the Indonesian island of Java periodic, long-continued human firing of vegetation has been the greatest menace to its forests (Shuitemaker 1950 in Bartlett 1955). Through repeated burning the tropical forests around the world have been reduced in area and often replaced by savannas and grasslands (de la Rue 1958; Batchelder and Hirt 1966; Walter 1971).

For more than a century observers and researchers have recorded and documented tropical man's often careless and negligent use of fire. Using the cumulative written work of many of these scientists, we have put together a general scenario, based upon a myriad of specific cases, about how fire has contributed to forest destruction in the tropics.

Batchelder and Hirt (1966) wrote:

because the number of interrelationships among fire, man, and [the] environment are nearly infinite; no one condition or set of conditions can be assumed to be dominant for all parts of the tropics.

We understand and heartily endorse this observation. As a result of the pantropical view we have taken, our generalizations are not necessarily appropriate to all tropical ecosystems, macrosites, and microsites. The information we are providing, while valid in general, must be checked against site specific conditions. Undoubtedly, tropical forest land managers and policy makers have a great and present need for extensive and intensive research about fire behavior and fire effects in their forests.

TROPICAL FOREST LOCATION

Tropical forests are located in lowland elevations -- generally below 1300 meters -- of the large, global belt around the equator, primarily between the Tropics of Cancer and Capricorn. Where tropical climatic conditions extend beyond the north and south tropical latitudes, so do the tropical forests. The forests are concentrated in Africa and the Americas with more than half of the closed forests located in South and Central America. The forests of the Amazon River drainage account for the bulk of the New World's closed forest. In contrast the vast majority of open tropical forests are located in Africa (See table 1).

TROPICAL DEFORESTATION

Estimates of tropical forest area range from 15 million to 19 million square kilometers -- approximately 42 percent of all tropical land and 13 percent of the earth's land surface. Closed forests -- those with a continuous canopy -- account for about 9 to 11 million square kilometers (UNESCO 1978). Deforestation rates for the closed forests are largely hypothetical and vary with the estimator and the definition of deforestation used. Stated loss rate figures run from 100,000 to 245,000 square kilometers per year (Myers 1981).

Geographically, the losses are pantropical. The pressure on the forests is greatest at the forest edge where they are most accessible. This edge can be a broad ecotonal belt or an abrupt boundary.

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Table 1. Global location of tropical forests by percent of total tropical forest area (U.S. Interagency Task Force 1980).

Type of Forest (pct)	Location
All Tropical Forests (1.9 billion hectares)	
42 percent	South and Central America
37 percent	Africa
21 percent	Asia/Australia/Oceania
Closed Tropical Forests (1.1 billion hectares)	
50 percent	South and Central America
30 percent	Africa
20 percent	Asia/Australia/Oceania
Open Tropical Forests (0.8 billion hectares)	
64 percent	Africa, Asia, Australia, Central and South America

Primary deforestation activities are industrial logging, fuelwood gathering, and agricultural clearing. Of these three, destruction associated with the forest farmer is the most important; and the forest farmer's primary tool is fire (Nichols 1901; Budowski 1956; Denevan 1978). Some overlap in deforestation activities does exist. For example forest farmers often move into logged areas to establish their farm plots.

In using the term forest farmer we mean the traditional shifting agriculturalist as well as the modern "pioneer" farmer-settler. Development, greater rural population densities, and the demands of a market economy have in many places changed subsistence shifting agriculture so much that ecologically it is not much different than the farming practices of the pioneer settlers.

FLAMMABILITY OF TROPICAL FOREST TYPES

In the tropics the climatic regulators of vegetation type are the amount of rainfall during the wet season and the duration and intensity of the dry season (Walter 1971). Three general forest types are relevant to our look at anthropogenic fire and deforestation. In order of most rainfall and shortest dry season they are: the tropical rain forest, the semi-deciduous forest, and the deciduous forest (Mueller-Dombois 1981). Deciduous forests can be further divided into moist and dry forests (Walter 1973). The moist deciduous forests receive more rainfall than the dry deciduous forests and grow on soils with greater water-holding capacity. Rain, semi-deciduous, and moist deciduous forests are closed forest types. Dry deciduous forests are open types.

The three closed forest types are fire independent ecosystems (Vogl 1977). Successful natural ignitions are rarely sustained. Low light levels on the floor of the closed forest during the growing periods prevent growth of significant amounts of herbaceous vegetation. High temperatures and moisture levels promote rapid decay of litterfall. Furthermore, low fuel loading and large fuel size, high moisture content, and wide fuel spacings, combined with the high ignition temperature typical of most tropical forest fuels, mitigate against prolonged, continuous combustion in the undisturbed closed forest (Batchelder and Hirt 1966; Trollope 1980). Open forests do have herbaceous and shrub understories because light penetrates to the forest floor.

Once the undisturbed closed forest is cleared, though, xeric understory and overstory species become established on the site and at the forest edge. This secondary vegetation is more likely to sustain combustion if ignited. After fire has invaded the forest once, the forest remains in constant danger from human set fires (Spurway 1937; Aubreville 1947; Budowski 1966).

Flammability of Tropical Rain Forests

The tropical rain forest is evergreen or mostly evergreen. Though there is no true dry season, there can be a relatively dry period in this forest type. Even in such a "dry" period precipitation averages at least 100 millimeters per month. Mean annual temperature hovers around 24 degrees Celsius. Decomposition rates are rapid, so there is only a thin litter layer on the forest floor at any given time. Primarily due to its high moisture level, the undisturbed tropical rain forest is almost fireproof. Once the forest is opened, though, it becomes susceptible to burning. Dead and live vegetation in the opening and at the forest edge quickly dry upon exposure to the intense tropical sun, thus becoming more flammable. Under these circumstances the tropical rain forest will burn.

Flammability of Semi-deciduous and Deciduous Forests

The semi-deciduous and deciduous forests are seasonal forests because they exist in the alternating climates of wet summers and dry winters. The number of dry months varies from roughly three to six in the semi-deciduous forest, six to eight in the moist deciduous forest, and eight to ten in the dry deciduous forest (Walter 1971). Mean temperatures range between 20 and 28 degrees Celsius.

The alternating wet and dry seasons is conducive to fire occurrence. During the wet season there is substantial plant growth which dries in the dry season. The deciduous plants not only dry out, but also shed their leaves. Nevertheless, like the rain forest, the semi-deciduous forest ordinarily does not burn easily. If this forest is opened to the sun's insolation, however, its vegetation dries, becomes more flammable, and, therefore, more likely to burn if exposed to an ignition source.

The deciduous forest is more susceptible to burning in its unaltered state (Walter 1971, 1973). As the dry period grows longer and more severe, greater numbers of deciduous tree species and fewer evergreen species occupy the forest while total tree density decreases. The deciduous forest, especially the open forest, has greater fuel accumulations due to abundant litterfall and the curing of grasses and other low understory vegetation during the dry season. Exposed to the tropical heat, these fuels quickly desiccate. Under these circumstances there are sufficient fuels of small size, low moisture content, and close spatial arrangement to carry a surface fire when fire enters the forest. As the dry period grows longer and more intense, the potential fuels become more flammable and the fire danger is magnified.

The fuel complex and fire potential of tropical forests are altered by human activity that removes the vegetation, thus creating openings in the forests. After the initial clearing fuel loading increases in all size classes, scattered evenly over the site. After a variable period of exposure to solar heating these fuels dry sufficiently to burn. In the following years grasses and other herbaceous vegetation, as well as woody species, occupy the site as pioneers in secondary succession. This vegetation, adapted to drier, open environments, grows more or less evenly over the site and dries rapidly in the absence of precipitation. These early successional conditions provide a fuel complex that will burn without cutting and extended drying (Vogl 1969; Walter 1971). If disturbed forest sites are repeatedly burned, highly flammable, quickly regenerating grasses such as *Imperata* species rapidly dominate the site; creating an easily burned, self-replacing fuel complex.

THE PROCESS OF DEFORESTATION BY FIRE

Anthropogenic fire is concentrated in the open and ecotonal areas of the tropics where humans live and work. Annually, sometimes more often, and usually at the end of the dry season, residents set their fires. Generally, these are surface fires which are carried by ground litter and herbaceous and shrub vegetation. Fire intensities are usually low due to low available fuel loadings, high fuel moisture and relative humidity, and discontinuous fuel spacing. Fire fronts are typically shallow and narrow. Areas burned are normally small and patchy (Batchelder and Hirt 1966).

These fires pose two major problems important to deforestation. Foremost, with some exceptions, few people make any attempt to control their fires. They simply rely on the low flammability of surrounding green vegetation to contain the fires. This lack of concern about fire control is all too common throughout the tropics.

The second problem is a result of the first. Too many fires escape the intended burning area. Cook (1909) observed that fires were usually allowed to spread wherever fuels would carry them. As the population density of forest farmers increases, abandoned and productive agricultural plots remain in close proximity (Denevan 1978). Abandoned plots are frequently composed of xeric secondary vegetation that readily burns during the dry season. Fires intentionally set in the productive plots accidentally burn into the nearby abandoned plots. These escaped, uncontrolled, human set wildfires eventually spread into the adjoining forest. This scenario accounted for nearly 100,000 hectares of wildfires in Mexico's eastern Yucatan Peninsula during the summer of 1989 (National Fire Protection Association 1989; Garrett 1989).

The actual process of deforestation by fire has been described by several authors from Cook in 1931 to Mueller-Dombois in 1981. Fire originating in adjacent open areas burns to the forest border. Depending on the intensity of the fire, density of the vegetation at the forest edge, fuel loading, and forest moisture conditions, fire may or may not penetrate the forest. Under normal circumstances fire will not enter a rain forest, but fires can burn from several meters to 1 or 2 kilometers into the semi-deciduous and deciduous forests. Once at or within the forest edge, fire intensity lessens as available fuel decreases and relative humidity increases. Fire damage is usually minimal. Herbaceous growth, coppice stumps, low bushes, suckers, and seedlings are killed and varying amounts of duff and litter are removed by the fire. Saplings and some fire sensitive species may be killed. Also, larger trees may be scorched or scarred around the butt.

The killing of undergrowth and trees in the burned forest area opens more of the forest to direct sunlight. Grasses quickly establish and rapidly grow in the sunlit areas. In forests which adjoin annually burned savannas or which surround annually burned openings, the invading understory vegetation provides the fuel that will allow the next season's fires to spread farther into the forest. Furthermore, opening of the forest edge to greater sunlight alters the edge microclimate to a drier type which also may contribute to increased intensity of the next fire.

LONG-TERM EFFECTS OF UNCONTROLLED FIRE USE

The forest vegetation shields the soil and the site from the drying effects of the sun and wind. Repeated fires open forests and expose the forest soils by removing living vegetation and litter. Soil surface temperatures rise and relative humidity decreases in response to direct solar exposure. Addition of new organic matter is reduced. Given these conditions, the closed nutrient cycling system of the tropical forest is damaged. Movement of essential nutrients to the forest vegetation is interrupted (Richards 1951). Wind and solar insolation desiccate the exposed soil and contribute to increased evapotranspiration which further reduces soil moisture. Microorganism populations shrink as organic matter content causes reduced nitrogen fixation and nutrient mineralization. Soil impoverishment is the result (Camero-Zamorra 1952).

The combined effect of repeated firing, insolation, and torrential rains is a breakdown in soil structure. Under these forces the soil disaggregates and compacts (Pittier 1939; Jha and others 1980). Soil density increases and porosity decreases leading to reduced soil moisture holding capacity. In the oxisols, ultisols, inceptisols, and the red earths typical of the humid and seasonal tropics a hardpan may develop if exposed to repeated wetting and drying (de la Ruc 1958; Donahue and others 1977). Once exposed to the elements, erosion of the fragile topsoil becomes a serious problem.

With progressive opening of the forest microclimate warms and dries, soil moisture and fertility decline, and less demanding woody and herbaceous plants adapted to drier conditions become established (Budowski 1956). Forest vegetation that survives the repeated fires or degraded site conditions lingers on singly or as relict groves and gallery forests (Batchelder and Hirt 1966). Forest regeneration that overcomes the poorer site conditions is either killed during regular burning or suppressed by the invading vegetation which is more fire-resistant (Innes 1971; Vogl 1977). Eventually, even the most fire-resistant woody species are eliminated. At this point the forest site is totally degraded and deforestation is complete. Continual firing will prevent the return of forest growth to formerly forested sites.

MANAGEMENT OF ANTHROPOGENIC FIRE

The challenge is to halt haphazard fire use without prohibiting rational use of fire for legitimate agricultural and non-agricultural land management. However, since fire is the primary land clearing tool of most agriculturalists, implementation of a rational fire management program will be a difficult and sensitive task. Human use of fire can never be successfully eliminated, nor is its prohibition necessarily desirable. A fire management program, while serving to preserve and protect tropical forests and human welfare, must respect the basic rural cultural foundations on which burning rests. It must also allow for inevitable and unavoidable economic use of forests and grasslands.

Governments of countries with tropical forests have become more aware of the forest fire problems they face and of the need to protect their forest resources. We suggest that the first task in dealing with the fire problem should be the formulation of a national fire policy to provide a framework for further actions. Every nation has a unique fire situation, and each nation's fire policy should reflect that uniqueness. In every case, though, the all-important human dimensions of fire must be addressed. Human-caused fires are preventable, but fire policy that threatens traditional land uses will ultimately fail.

To bring anthropogenic fire under control the affected people must understand and support management programs. Education is essential to impart understanding and to change the attitudes of fire users toward fire and the environment. Hand in hand with an educational effort, an agricultural or forestry extension program could be established to instruct users about the correct application of fire and its positive and negative effects on the land and its vegetation. The negligent and indifferent fire habits so common in the tropics must be reformed for a program of managed fire to be successful.

Education is a long-term solution to a pressing problem; nevertheless, the best of intentions, the finest policy statement, and the most modern science and technology will avail us little if the attitudes of fire users remain unaltered. Mr. Helmut Haufe, FAO Regional Forestry Officer in Latin America, stated that anthropogenic wildfires in too many cases are "due to the lack of a proper information and instruction system" (pers. comm. 1981). Mr. Haufe's statement is a significant endorsement for an extensive and vigorous fire education program.

Other actions that may help manage the anthropogenic fire problem are more appropriately considered under the headings of agricultural and rural development, but bear mentioning

here. These actions include providing alternatives to traditional agricultural practices and incentives to take up the alternatives. The already mentioned extension programs could help develop and promote alternative methods and technologies. Land use, tax, rural development, and internal colonization policies can also be adjusted to reduce the motives for negligent and abusive fire use.

CONCLUSION

In 1967 Batchelder wrote that the "use of fire in the tropical world is no longer in a stage of 'ecological climax' wherein a stable, harmonious relationship to the environment exists." In fact over the past hundred, if not several hundred years, the careless and repeated use of fire has resulted in ecological disturbances which have steadily forced the retreat of tropical forests worldwide. Natural succession, which normally heals ecological wounds and returns ecosystems to their predisturbance states, has been halted by the frequent and often devastating nature of anthropogenic fire. Insofar as tropical forest regeneration is concerned, continuous anthropogenic fire disturbances are unnatural and, therefore, beyond the adaptive and recuperative powers of forest ecosystems. Repeated burning leads to replacement of the original vegetation by a series of seral communities more easily burned until a fire disclimax community is finally established.

In a paper delivered to the West Indian Agricultural Conference in 1901 Nichols called for an immediate end to uncontrolled burning in the tropics. Ninety years later a great variety of voices still echo his call. Since 1901 efforts to reduce the frequency and effects of anthropogenic fire in the tropics have failed. The burning continues. Effective fire management policies, that are strong on education must be developed and implemented. Without them increasing population, development, and colonization pressures within the tropical forest regions will assure the unabated cultural use of fire in its present destructive form.

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WILDFIRE IN THE PALEOZOIC: PRELIMINARY RESULTS OF A CASE STUDY ON THE FIRE ECOLOGY OF A PENNSYLVANIAN FLOODPLAIN FOREST, JOGGINS, NOVA SCOTIA, CANADA

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Abstract—Sediments of the Joggins Section, Cumberland Basin, western Nova Scotia accumulated in lowland forests approximately 300 million years ago. The 4,000-meter-thick sedimentary sequence includes channel and overbank sandstones interbedded with stacked immature paleosols developed in thick mudstone horizons. Fusain (charcoal) is common in all sedimentary facies present at Joggins. Fusain occurs as isolated macroscopic clasts and also as recognizable layers of clasts and particles within the mudstone/paleosol facies. These layers are interpreted as fire-event horizons. In one example, an ancient tree, rooted below a fire horizon, is preserved with its charred periderm intact. Palynological analysis shows that there is an increase in taxonomic diversity immediately following this fire. Although arborescent lycophytes remain dominant in the palynoflora, cordaitan and medullosan gymnosperms enter the postfire community. These groups decline later as prefire vegetation is reestablished. Numbers of fern-spore species increased following fire, although ferns did not become more abundant. Studies of fire-related floristic patterns preserved in the fossil record can test ecological generalizations and theory derived from present day ecosystems and may help ecologists understand the role of changing fire regimes in long term vegetational change.

INTRODUCTION

The classic image of Carboniferous lowland ecosystems is a static and steamy tropical wetland. Groves of arborescent lycophytes with their understory of tree ferns and pteridosperms (seed-bearing plants with fern-like foliage) stand in ever-wet soils, while along the riverbanks clumps of sphernopsids flourish. Stutzer and Not (1940) wrote: "It is difficult to believe that such a thing [wildfire] happened in view of the moist condition of the Carboniferous forests. Judging from the plant associations that grew there, fires could not have spread rapidly in a swamp forest." However, Izlar (1984) reported that portions of the Okefenokee Swamp-Marsh Complex burn every 25 to 30 years, and that this fire regime maintains the floral composition and heterogeneity characteristic of the ecosystem. As our understanding of wetland ecosystem ecology develops, we are called to reevaluate our view that ancient swamp and floodplain ecosystems were static. We must reexamine the role of fire in these systems.

For this reason, I have begun a study of community dynamics and fire ecology in the Joggins Section (Middle Pennsylvanian) of western Nova Scotia, Canada. This paper reports on the initial study testing the feasibility of detailed ecological reconstruction of this ancient ecosystem. In this paper, I will: (1) show that ecological-scale resolution of the fossil record is possible in this stratigraphic section; (2) establish that wildfire was a significant factor in this ancient ecosystem; and (3) demonstrate that wildfire may have, in part, controlled the distribution of some floodplain plants.

GEOLOGIC SETTING

The Joggins section is located in the Cumberland depositional basin of western Nova Scotia, Canada (fig. 1). Approximately 4,000 meters of sediment arc well exposed in a continuous cliff outcrop along the eastern shore of Chignecto Bay. The outcrop face is approximately perpendicular to strike; bedding dips range from 15° to 20° south. Sediments are Middle Pennsylvanian (approximately 305 m.y.b.p.), and have been biostratigraphically dated as latest Westphalian A through earliest Westphalian C using miospores (G. Dolby, unpublished data). Joggins sediments are well correlated with other terrestrial and marine deposits in the North American midcontinent, the Appalachians, and Europe (Phillips and others 1985).

The 4,000 meters of sediment exposed at Joggins record 2 to 5 million years of history (Harland and others 1989). The inferred rapid sedimentation rate suggests that decade-scale or finer stratigraphic resolution may be possible at Joggins. Such fine time-scale stratigraphic resolution is essential for the study of community dynamics and responses to disturbance in an ancient ecosystem. Without adequate time-stratigraphic resolution the record of ecological-scale processes will be obscured by the homogenizing effect of slow sedimentation.

The Joggins stratigraphic sequence consists of channel, levee, and overbank sandstones, floodplain mudstones, and thin coals probably attributable to floodplain ponds. Fluvial facies were deposited in an anastomosing river system that drained the Cobequid Highlands to the present-day southeast (Rust and others 1984). Thin, organic-rich lacustrine limestones also occur in the lower portions of the section. I have observed

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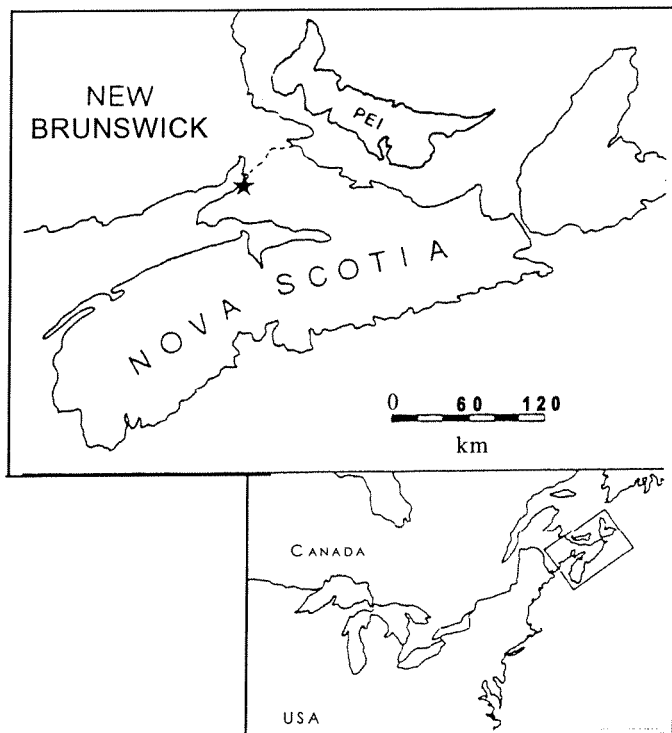


Figure 1 --Location of the Joggins Section area.

no evidence of marine facies or marine influence on terrestrial facies at Joggins. Within the Joggins Section sediments tend to redden and sandstones to coarsen up-section. Rust and others (1984) concluded that these trends indicated a tectonically mediated steepening of the alluvial plain, which lowered relative water table and increased the amount and grain-size of transported sediment.

For this study, the clastic floodplain mudstone/paleosol facies are of particular interest. Mudstone horizons vary from 1 to 20 meters in thickness and are interbedded with crevasse-splay and channel sands. In lower portions of the section, mudstones and paleosols constitute 70 to 80 percent of the stratigraphic section. Color of mudstones varies from gray-green to mottled to gray-red or red up section, corresponding to the inferred water table gradient. Despite this general trend, there is substantial color variation on a finer stratigraphic scale within the section. Mudstones are commonly very poorly-bedded to structureless with moderate to well-developed immature paleosols. Paleosols are characterized by root traces and localized root casts, siderite rhizoconcretions, and locally developed soil structures. Recognizable soil horizons are commonly absent or poorly developed; paleosols generally have uniform texture vertically. Upright trees are commonly preserved as partial sandstone molds within mudstone facies. These trunks may be partially filled or cast in mud, commonly with a rind of vitrinite coal, which is the preserved remains of the lycophtic tree's thick periderm.

Together, these observations suggest that floodplain mudstones were deposited in frequent (geologically speaking) flooding events that emplaced small amounts (centimeters) of

fine-grained sediment, rather than in catastrophic events depositing tens or hundreds of centimeters of sediment. Under this depositional regime, elastic swamp trees would not be substantially disrupted by sedimentation events, but, continual redefinition of soil surface by sediment input would cause successive readjustment of soil profile and lead to the observed lack of well-developed horizons. This model fits well with observations of modern tropical rivers such as the Brahmaputra in India and Bangladesh (Coleman 1969) and the Orinoco in Venezuela (Armando Torres, 1991, personal communication).

During deposition of Joggins sediments, the Pennsylvanian Maritimes Basin was near-equatorial and had a tropical to subtropical climate (Rowley and others 1985, Galtier and others 1986). Ziegler and others (1981) reconstructed this region at about 1.5° north latitude and in a zone of Easterlies. Peat-forming ecosystems at Joggins and in the Springhill coal field to the east are interpreted as groundwater-influenced (rhicotropic), rather than raised, bog systems (Calder and others in press). Groundwater-fed systems occur in the East African rift, where availability of moisture varies seasonally (Cecil and others 1988). If rhicotropic bogs occurred in Nova Scotia during the Pennsylvanian, it is possible that they, too, formed under conditions of seasonally varying moisture availability. However, Cecil and others interpreted the Westphalian B as equitably and adequately wet, based on the relative abundance of ombrotrophic versus rheotropic bogs in the central Appalachians. Conversely, Phillips and Peppers (1984) interpret the Westphalian B as drier and more seasonal than the preceding and succeeding epochs based on swamps in the North American midcontinent. Rowley and others (1985) reconciled these interpretations by suggesting that an increasingly monsoonal climate coupled with the orographic effect of the developing Appalachian highlands to the southwest of the Canadian Maritimes Basin created regionally different rainfall patterns across the Euramerican coal province. In the Maritimes Cumberland Basin, higher paleolatitude and the presence of highlands to the east could further intensify such a regionally seasonal climate.

The Joggins fluvial sandstones provide direct sedimentological evidence for fluctuating discharge that suggests seasonal rainfall. Multistoried sandstones, graded pebbly sandstones, scour fills, conformable mud drapes, and fan sheetflow in overbank deposits all point to variability in stream discharge, which is consistent with the monsoonal interpretation. However, it is impossible to determine from sedimentological evidence alone whether flood events occurred with seasonal or decade-scale frequency. By either interpretation, though, the ancient landscape at Joggins experienced periods when evapotranspiration exceeded precipitation, thus allowing fuels to dry sufficiently to permit wildfire. In this respect, the climate-induced fire regime may have been quite similar to that in the Okefenokee swamp (Izlar 1984) or the Orinoco floodplain.

EVIDENCE OF WILDFIRE ON THE JOGGINS FLOODPLAIN

The presence of fire in the Joggins ecosystem is inferred from the presence of fusain (charcoal) throughout Joggins sediments. Fusain occurs at Joggins in several sedimentary contexts. In coals, fusain occurs as discrete layers that are laterally continuous for meters on the scale of the outcrop. Within these horizons, fusain may occur as discrete, macroscopic clasts or in a mechanically ground, powdery form. Within the mudstone/paleosol facies, fusain also occurs as clasts distributed in discrete, sharp-bounded horizons that can be traced laterally for meters along the exposed outcrop. Clasts occur in a matrix of finely-ground charred material with varying amounts of clay. Fusain clasts varying from a few millimeters to 50 centimeters (fig. 2 a-c) are also common in the sandstones and siltstones associated with channel facies. The largest fusinized logs show a perpendicular surface fracture pattern consistent with charring by fire. In the reddest sandstone facies, charred logs are common in mud drapes of channel fill and in point-bar deposits.

The origin of fusain and related materials described from coal macerals has been the subject of much debate between workers who favor a pyrolytic origin for this material and others who believe fusain is produced by some unknown slow oxidization process. Scott (1989) reviewed the evidence and arguments and concluded that most fusain found in the Paleozoic and Tertiary rock record is the direct result of surface burning of vegetation or other surficial organic material. Ting (1982) agreed: "Fusinite and semifusinite are derived primarily from woody tissues charred or partially charred during swamp fire. Once charred, the fusain progenitor--charcoal--becomes extremely stable and inert to any chemical and biochemical attack and is thus well preserved. Some coal beds may contain 20-25 percent fusinite, occurring in numerous fusain bands that suggest frequent swamp fires during peat accumulation." Cope and Chaloner (1985) added that wildfire was an important ecological factor since the evolution of a land flora in the Silurian and Devonian. In accordance with these conclusions, I adopt the charcoal interpretation of fusain and will refer to fusain as fossil charcoal.

METHODS FOR POLLEN ANALYSIS

The samples analyzed were collected stratigraphically above and below a horizon of fusain clasts, mechanically disaggregated charcoal, and clay associated with the preserved stump of an ancient tree (fig. 2 d-e). The stump, which is located about 150 meters south of McCarren Creek (Rust and others 1984), is preserved in mudstone/paleosol capped by an overbank sand body. The locality is in the lower portion of the section measured by Rust and others (1984) but is not noted in their published stratigraphic section, probably because cliff-face erosion had not yet exposed the stump at

the time of their field work. When collections for this study were made (August, 1989), the stump was badly eroded, but periderm material preserved as fusain rather than vitrinite was clearly visible and the outline of the enlarged base of the tree was easily traceable to a well-defined and laterally continuous horizon of fossil charcoal.

Based on the abundance of centimeter-sized fusain clasts within the mudstone/paleosol facies, this horizon is interpreted as a fire event horizon that records a single wildfire in an ancient stand. This conclusion is based on analogy with studies of Recent sediments, which show that even in lakes, where in situ deposition is less likely than on the floodplain environment, peaks in charcoal abundance can be correlated with single fire events within the drainage basin and charcoal clast size can be related to transport distance (Clark 1988, 1990).

A mudstone sample from below the charcoal horizon sampled prefire vegetation. Stratigraphically successive samples were taken at 1-centimeter intervals above the fusain layer. Samples were processed according to standard palynological technique (e.g. Traverse 1988). Rock was degraded in concentrated hydrofluoric acid; unwanted organic material was oxidized with HCl and bleach; clay was removed by heavy liquid separation with ZnCl₂. Strew slides were made with glycerin jelly. Each slide was scanned systematically and each palynomorph encountered was recorded by genus. Species-level diagnosis was made only for the most abundant spore genus, *Lycospora*, the spore of several arborescent lycophytes. In each sample, 400 palynomorphs were counted and taxa relative abundances were calculated. Following the count, each slide was scanned for additional rare forms. Relative abundance is plotted by stratigraphic position to yield standard pollen diagrams (figs. 3 and 4).

When interpreting a palynological analysis, one must keep in mind several caveats. First, differing quantities of pollen and spores are produced by different taxa. Wind pollinated plants, for example, produce prodigious amounts of pollen and spores while partially or wholly entomophilous plants will be relatively underrepresented in the dispersed pollen and spore record. This caveat is traditionally reconciled by admitting that palynomorph relative abundance cannot be translated directly into quantitative stand measures such as standing biomass or DBH. In the modern pollen record, differential spore production can be a significant confounding factor. However, entomophily was probably less important in the Carboniferous than among modern angiosperms. Consequently, one might expect pollen and spore relative abundance to be a better proxy for individual plant relative abundance in these ancient forests. It is also possible to develop conversion factors that will allow pollen and spore abundance to better approximate other measures of stand composition. This approach has been successfully applied to Pleistocene and Recent stands (Davis and Goodlett 1960).

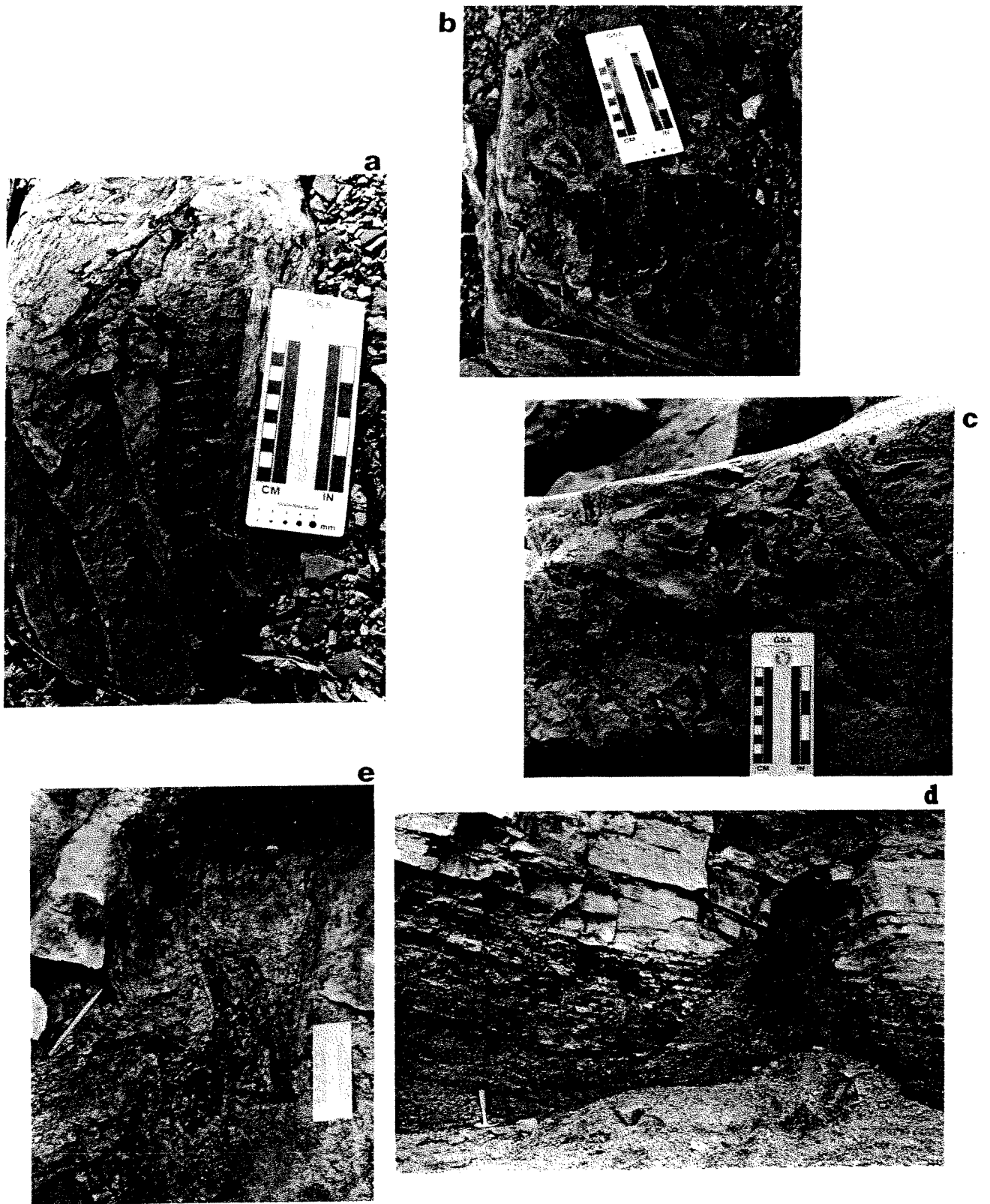


Figure Z.--Physical evidence for fire in Joggins Section rocks. (a-b) Compressions of fusinized (burned) wood in fine-grained sandstone associated with a channel deposit, Spicer's Cove. Note perpendicular fracture pattern characteristic of burned wood. (c) Charcoal fragments and impressions of unburned plant axes in channel sandstone. Arrows indicate charcoal fragments. (d-c) Tree cast with burned periderm. (d) Extensively eroded outline of tree stump showing outline of tree base extending to dark, charcoal-rich horizon (at hammer shank). Palynological samples taken one meter to the left of hammer position. (e) Close-up of burned trunk. Pen and arrow indicate fusinized material.

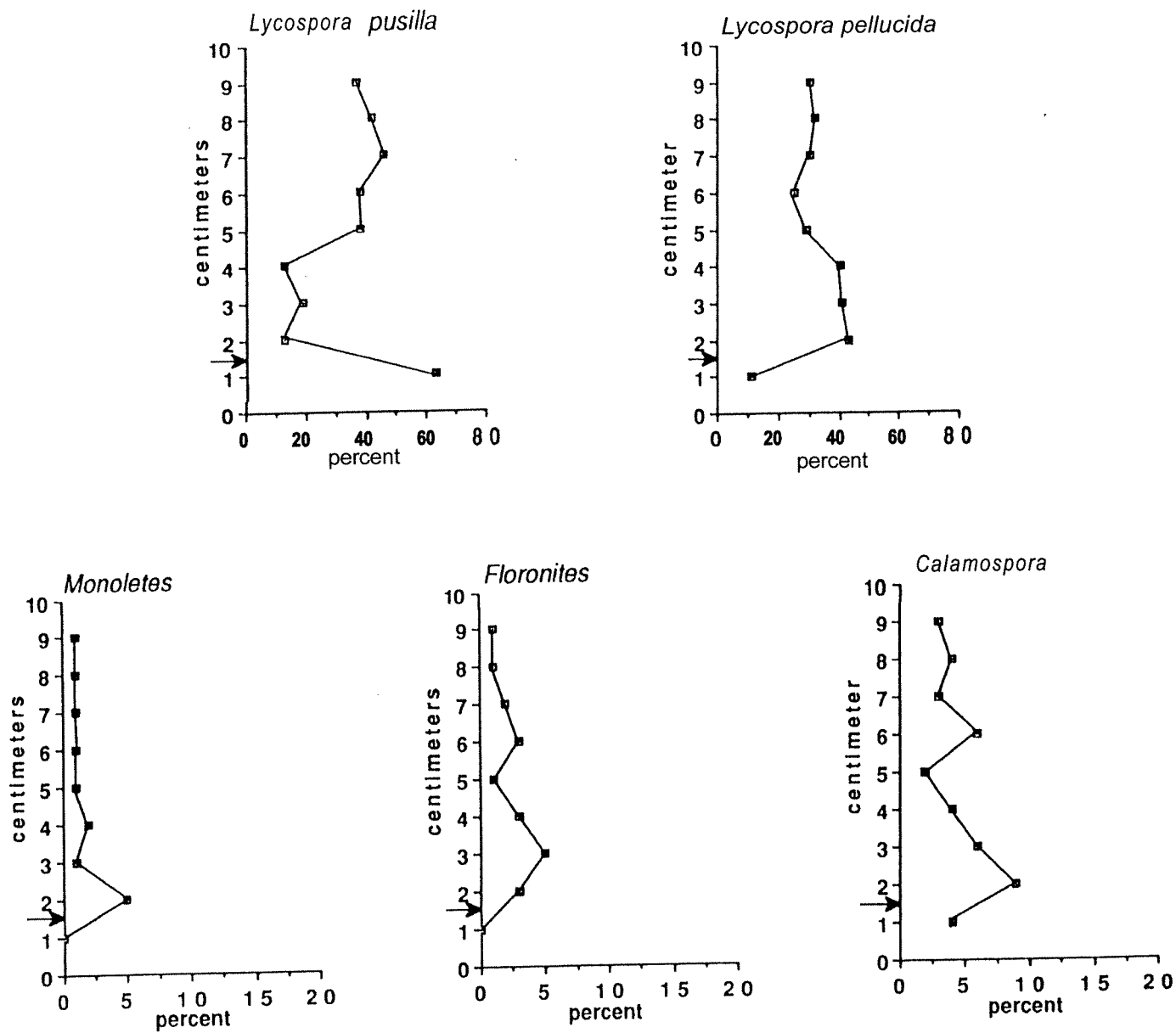


Figure 3.--Relative abundances of several palynomorph taxa. Arrows indicate stratigraphic position of fusain horizon.

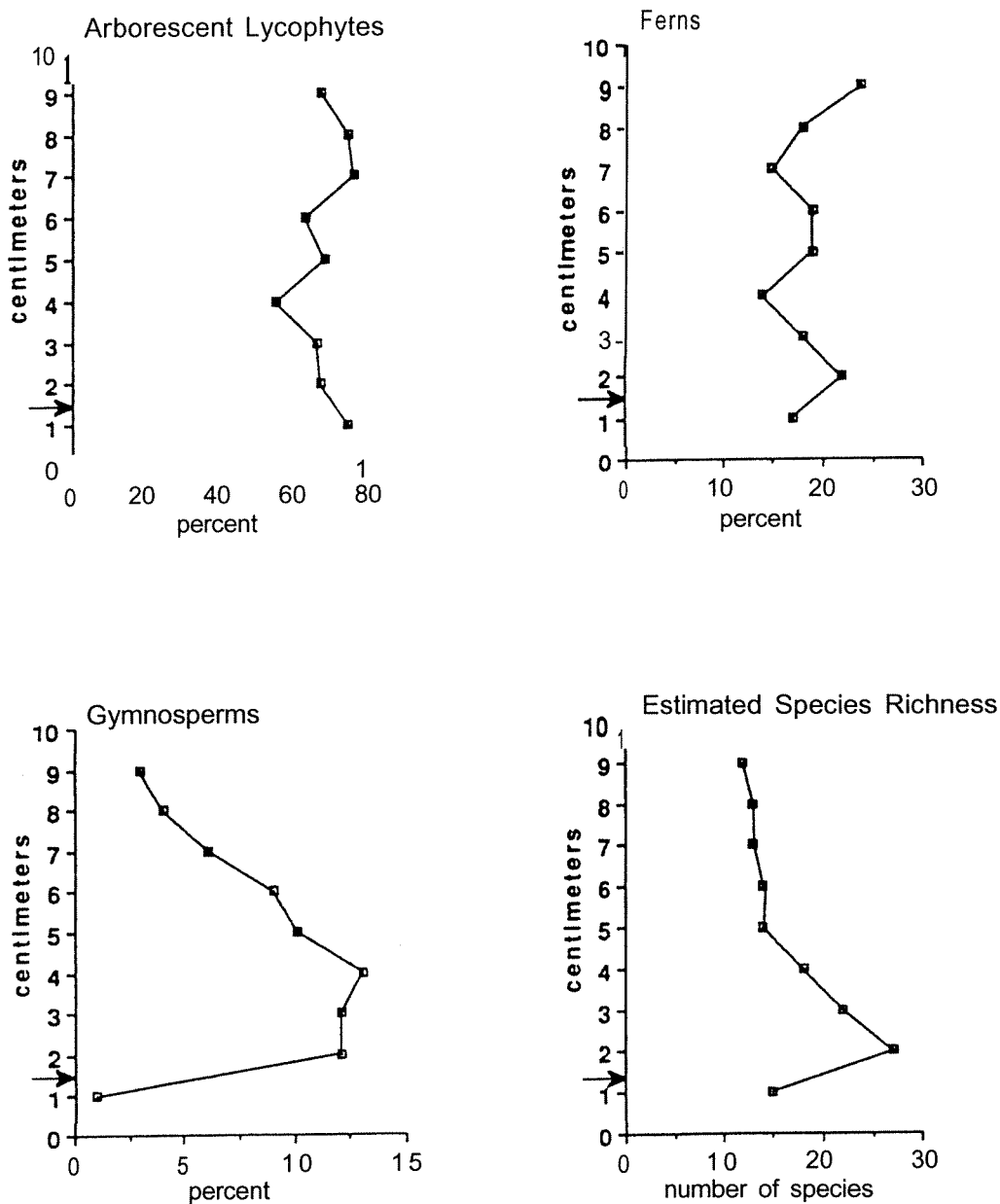


Figure 4.--Relative abundances of major plant groups and estimated species richness. Arrows indicate stratigraphic position of fusain horizon.

However, such conversions are only now being developed for the Carboniferous (Willard 1986). Future interpretation of these communities will incorporate this more quantitative approach to stand composition; however, that is beyond the scope of this preliminary study. Second, changes in pollen and spore abundances do not necessarily mean a change in stand composition. Some modern plants are stimulated to reproduce by disturbance, thus enriching their representation

in the dispersed pollen and spore record. At this stage of the study, this influence cannot be discounted, but at the scale of stratigraphic resolution applied in this paper, pollen and spores are regarded as good indicators of standing vegetation (Davis and Goodlett 1960). Clearly, one must tailor questions asked of the pollen record to the time-stratigraphic, taxonomic, and quantitative resolution appropriate to the data.

RESULTS

The spore species Lycospora pusilla, produced by some arborescent lycophytes, was most abundant (63 percent) in the prefire vegetation (fig. 3). The other arborescent lycophyte spore present (Lycospora pellucida) represented only 10 percent of the palynoflora. Lycospora is produced by a number of species in the stem genus Lepidophloios. Other palynomorphs including Calamospora, the spore of the sphenopsid Calamites, and a complex of ferns made up approximately 10 and 15 percent of the palynoflora respectively. The pollen of gymnosperm taxa including Monoletes, the pollen of medullosan pteridosperms, and Florinites, pollen of the conifer relative Cordaitea, were not present in the prefire palynoflora. A simple count of palynomorph taxa suggests that about 15 species were present. This estimate of species richness (fig. 4) is tentative and pending more complete taxonomic study of the palynoflora. Note also that, in some cases, a single spore and pollen taxon was produced by more than one megafossil taxon, thus under-representing species richness.

The sample collected stratigraphically immediately above the fire horizon shows several important changes in the palynoflora. Abundance of Lycospora pusilla declined dramatically from 63 to 13 percent. Conversely, L. pellucida increases from 11 to 43 percent. The increased relative abundance of L. pellucida is not entirely a relic of decline in abundance of L. pusilla; L. pellucida becomes absolutely more common in an average microscope field on slides of comparable palynomorph density. Fern spores and Calamospora become more common above the charcoal horizon. Medullosan and cordaitan gymnosperms also appear to enter the community following fire. The medullosan seed fern pollen, Monoletes, reaches its greatest abundance (6 percent) immediately above the fire horizon. Estimated species richness also reaches maximum (approximately 27 species) in the sample immediately above the fire horizon. This maximum includes several added rare or uncommon fern and herbaceous lycophyte taxa.

In stratigraphically successive samples above the fire horizon, several trends emerge. First, L. pusilla increases in relative abundance while L. pellucida declines until these taxa returned to approximately prefire levels. However, L. pusilla did not reclaim its prefire abundance within the sample interval. Likewise, L. pellucida declined in abundance throughout the sampling interval, but retained a higher postfire abundance (25 to 30 percent) throughout the sampling interval. In contrast with this gradual dominance exchange, Monoletes declined rapidly to a background abundance of 2 or 3 percent immediately after its abundance peak. Florinites, the pollen of cordaitan gymnosperms, increased in abundance more gradually to a maximum abundance in the second centimeter above the fossil charcoal horizon. Following this maximum, Florinites declined gradually to a background level similar to that of medullosan pollen. Species richness

followed a similar trend of steady decline to the prefire level in the fourth centimeter above the fire horizon. This decline is driven mainly by the loss of the rare and uncommon fern and herbaceous lycophyte taxa that appear immediately above the fire horizon.

DISCUSSION

Rapid and relatively continuous (perhaps seasonal) sedimentation is a prerequisite for ecological-scale resolution of the fossil record. The Joggins Section appears to provide such conditions; however, absolute sedimentation rates are difficult or impossible to ascertain. Consequently, one must look to the vegetation for confirmation of time scale. If the Joggins strata can be interpreted at the ecological scale of resolution, one should be able to detect vegetation change stratigraphically above sedimentologically-inferred disturbances such as fires. Similarly, ecological resolution should show gradual reestablishment of plant abundances similar to those seen before the disturbance. Clearly, these predictions are realized in this case. Figure 4 shows that arborescent lycophytes suffer a 20-percent decline in abundance following fire. Note that arborescent lycophytes with small, wind-dispersed microspores are likely to be over-represented in the postfire palynoflora due to spores transported from nearby, unburned stands into the gap. The lycophyte decrease in postfire samples is largely counterbalanced by an increase in gymnosperm+initially by medullosan pteridosperms and subsequently by cordaitans. Medullosans were characterized by large fronds displayed on an unbranched axis and minimal investment in low-density wood. Both of these features (minimal branching and low-density wood) are characteristic of modern colonizer trees in the tropics (Ashton 1978, Bazzaz and Pickett 1980, White 1983). Cordaitans have a more substantial structural investment in greater volumes of dense wood. These structural observations support the conclusion that medullosans, with their "inexpensive" construction, filled the colonizer role in these ancient communities, with the more structurally "expensive" cordaitans following in a mid-successional phase. Thus, the observed vegetation response, particularly the increase in gymnosperms, after fire establishes that ecological-scale changes are being observed; return to prefire abundances in stratigraphically subsequent samples reinforces the conclusion. These biological observations coupled with the inferred rapid sedimentation rate support an ecological-scale interpretation of the Joggins section. Thus, while I cannot conclude whether the sampled interval records decades or centuries in absolute time, the observed vegetation changes probably occurred within several generations of the plants involved--clearly an ecological-scale time frame.

If one accepts Scott's (1989) conclusion that fusain in coals and clastic sediments records wildfire, then it is clear from the abundance of fusain in the Joggins sediments that fire was not only present but common in the Joggins swamp

ecosystem. The influence of periodic fire on vegetation then becomes interesting. In a study of early Middle Carboniferous peat-forming mires, Phillips and others (1985) reported a correlation between an increased abundance of cordaitan gymnosperms and higher fusain percentages. In the upper "Pottsville" (Westphalian A/B correlatives) coals of northeastern Tennessee and eastern Kentucky, *Cordaitea* makes up 33 and 36.7 percent biovolume in coal balls with 9 and 7.4 percent fusain respectively. In the same region, two correlative coals with lower cordaitan abundances (1.7 and 14.3 percent) contain lower proportions of fusain (0.8 and 2.6 percent respectively). A similar pattern was observed in the Upper Foot Scam, Lancashire, England, the Buxharmont Scam in Belgium, and the Katharine Seam in the Ruhr, West Germany. Phillips and others (1985) conclude that this correlation reflects the cordaites' preference for drier habitats, which would be more prone to fire or other diagenetic oxidation.

The association of cordaitan gymnosperms with fusain is also observed in the Joggins fire horizon. In this case, however, detailed stratigraphic sampling shows that the cordaites were not simply growing in drier, fire-prone areas; rather, they were present in the community only after fire and could not maintain a significant presence without further disturbance. This suggests that fire (or disturbance in general) was an important factor in controlling the distribution of this taxon in the floodplain community.

A clear fusain-abundance relationship for pteridosperms is not present in the data of Phillips and others (1985) from localities in the Euramerican Carboniferous. Medullosan pollen, *Monoletes*, is commonly not reported in standard palynological analysis because the large grains (100 to 200 micrometers) are eliminated from preparations by standard sieve techniques. Also, if the distribution of medullosan pteridosperms is patchy and ephemeral as hypothesized in this paper, its pollen might be easily missed in a grab-sampling regime. Consequently, absence of *Monoletes* from these reports (Phillips and others 1985) is not convincing evidence that pteridosperms were absent at those localities. At Joggins, however, the pollen of medullosan pteridosperms, like that of *Cordaitea*, enters the community and has an abundance peak immediately above the fire horizon. Again, these data suggest that the distribution of *Monoletes*-producing pteridosperms was influenced by fire. Arens (manuscript in preparation) notes that some of the medullosan pteridosperms show morphologic and distributional characteristics consistent with their interpretation as colonizers of disturbed habitats, while others appear to have been understory plants. While colonizer and understory medullosans cannot be distinguished by their pollen, the restriction of medullosans to immediately above the charcoal horizon at Joggins supports the conclusion that some medullosans functioned as colonizing plants that required disturbance (in this case, fire) and were unable to maintain their presence (or at least to reproduce) on a site without subsequent disturbance. This conclusion can easily be

reconciled with Phillips and others (1985); medullosan pteridosperms were an ecologically and taxonomically diverse group, and summary data that include taxa from both colonizer and understory medullosan guilds would obscure a correlation between medullosan ecotypes and fusain.

Pollen analysis across the fire horizon clearly shows that there is a vegetative response to disturbance. Two important trends emerge. First, the lycophytes--dominant taxa before the fire--suffer a major decline after fire, but gradually recover prefire dominance. Second, the lycophytes were replaced in the postfire community largely by gymnosperms, primarily pteridosperms and cordaitans. However, these taxa apparently could not replace themselves on the site and eventually became locally extinct (Noble and Slatyer, 1980). Therefore, lycophytes and gymnosperms may also be filling different ecological guilds in the floodplain communities. The gymnosperms may represent key components of an early successional community that colonized habitat opened by fire; the lycophytes, then, constitute a later successional community that established in the shade of the colonizers and eventually succeeded to dominance in the area. Noble and Slatyer's (1980) model predicts that if fire occurs again during the gymnosperm stage of succession, medullosans and cordaitans will continue to exist on the site. However, in the absence of fire (or some other disturbance), the gymnosperms will become locally extinct and lycophytes will reassert community dominance. This latter prediction was confirmed in this sequence. The ephemeral distribution of early successional gymnosperms, particularly pteridosperms, is supported by observations in many Pennsylvanian-age lowland environments (Phillips 1981).

Species richness trends associated with disturbed ecosystems are equivocal. In the tropical rain forests of Uganda (Eggeling 1947) and old fields of Nigeria (Jones 1956) species richness is low during the colonization stage, peaks in mid-succession, and declines in late succession. This is inconsistent with the diversity peak observed immediately after disturbance in the Joggins sequence. One possible interpretation is that the initial, low-diversity phase was too brief to be resolved or was not recorded in this sequence. However, in the Yellowstone National Park forest ecosystem (Dale Taylor, 1990, personal communication), the Australian grassland (Burrows, in preparation), and chaparral (Zedler 1977) species richness is greatest immediately following fire, as in the Joggins floodplain community. In these cases, species richness is enhanced by the presence of several codominant species and a variety of less common species, much as in the Joggins sequence. This pattern is promoted by microenvironmental variation generated by heterogeneity in the distribution of plant resources such as light, moisture, and nutrients in the disturbed site (Bazzaz and Sipe, 1987). Analyses of more Joggins fire horizons will undoubtedly clarify the pattern of species richness following disturbance on the ancient floodplain, and permit more definitive interpretation.

FUTURE WORK AT JOGGINS

The research described here represents the first stage of a larger study of the Joggins plant communities. Conclusions presented are, therefore, more accurately described as hypotheses to be tested. The Joggins record presents an opportunity to use fine-scale palynological analyses to interpret the effects of disturbance on ancient plant communities. With analysis of more stratigraphic sequences spanning charcoal horizons, one may ask: (1) Is there a generalizable trajectory of vegetation replacement following disturbance in the Middle Pennsylvanian moist floodplain forests? (2) Does a similar pattern occur in contemporaneous peat-forming ecosystems? (3) Does this observed pattern change with sedimentologically-inferred differences in soil moisture? (4) What trends in diversity are observed within and between successional guilds in clastic floodplains and in peat-forming mires? Such an approach, emphasizing dynamic patterns within communities over time scales of several plant generation, offers the opportunity to test ideas of community stability and coherence suggested for the Carboniferous (DiMichele and others 1985, Phillips and others 1985). It also offers a new and different system to test similar ideas derived from and argued about by ecologists studying modern plant communities.

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FIRE HISTORY AND FIRE ECOLOGY IN THE COSTA RICAN PARAMOS

Sally P. Horn*

Abstract—The high peaks of the Cordillera de Talamanca in southern Costa Rica extend above timberline and support bamboo- and shrub-dominated páramo vegetation. The charcoal stratigraphy of sediment cores from glacial lakes reveals that fires set by people or lightning have occurred in the highlands for thousands of years. Historical sources and field evidence document numerous páramo fires since the mid-century. During the past 40 years, fire recurrence intervals at specific sites have ranged from 6 to about 30 years.

Patterns of postfire vegetation development support the initial floristics model of succession. The dominant bamboo (*Chusquea* [= *Swallenochloa*] *subtessellata*) resprouts vigorously following burning, as do associated ericaceous shrubs. *Hypericum* spp. suffer high mortality and recolonize by seed. Slow rates of growth and colonization by both woody and herbaceous species result in the persistence of bare patches of ground for a decade or more following burning.

INTRODUCTION

In a recent review of tropical alpine plant ecology, Smith and Young (1987) noted that fire is common on most tropical mountaintops. But the authors found few references on fire frequencies or fire history in tropical highlands, or on the impact of burning on vegetation, soil nutrients, and hydrology.

Since 1984 I have been working to fill this gap for the high mountains of southern Costa Rica. This paper summarizes the results of my research -- and that of U.S. and Costa Rican colleagues -- on fire history and fire ecology in the bamboo- and shrub-dominated páramos found above timberline in the Cordillera de Talamanca.

ENVIRONMENT AND VEGETATION

The uplifted granitic batholith that forms the backbone of the Cordillera de Talamanca is mantled by Tertiary volcanic and sedimentary rocks, which outcrop along with granodiorites and other intrusive rocks on the high peaks (Weyl 1957). About a dozen areas along the crest of the range reach above timberline, and support small to extensive stands of neotropical páramo vegetation (fig. 1). Many of these areas are quite remote and remain poorly known botanically.

Ecological research has focused on the páramos surrounding Cerro Chirripó (3819 m), the highest peak in Costa Rica, and Cerro Buenavista (3491 m). Glaciers occupied the upper valleys of the Chirripó massif several times during the Pleistocene, leaving behind a picturesque ice-carved landscape dotted by some thirty glacial lakes. The extensive (> 5000 ha) Chirripó páramo is protected within Chirripó National Park, which was established in 1975. Access to this remote

area is provided by rough trails that lead out of settlements on the lower foothills of the Cordillera de Talamanca.

The smaller (c. 1000 ha), unglaciated Buenavista páramo straddles the crest of the Cordillera de Talamanca along the Inter-American Highway route. There are no settlements within the páramo, but Cerro Buenavista is festooned with broadcasting towers, and jeep trails and electrical transmission line corridors crisscross the páramo. This area was the main route across the Cordillera de Talamanca even before the construction of the Inter-American highway in the 1940s, and the vegetation has long been affected by tree cutting, human-set fires, and grazing (Horn, 1989a). Janzen (1973a, 1983) believes that low forest, rather than páramo, covered the Buenavista peaks prior to extensive human disturbance.

In both physiognomy and floristics, the Talamancan páramos resemble the more extensive páramos of the northern Andes (Weber 1959), and most authorities consider them to mark the northern limit of páramo vegetation in the neotropics (Cuatrecasas 1979; Lauer 1981). The dwarf bamboo *Chusquea* (= *Swallenochloa*) *subtessellata* (Janzen 1983; Clark 1989; Horn 1989b) is a characteristic element within the páramos, forming monospecific stands in many areas (fig. 2). Woody dicots that grow intermixed with the bamboo include species in the Ericaceae, Hypericaceae, and Compositae families. A variety of herbaceous plants, many of Andean affinity, occur beneath the shrub canopy and in more open areas.

The oak *Quercus costaricensis* dominates the montane forests that are found just below timberline in the Buenavista and Chirripó highlands. The upper limit of oak forest ranges in elevation from about 3150 m to 3300 m. In some areas, oak forest 20-30 m high gives way to 1-3 m high bamboo- and shrub-dominated páramo along an abrupt boundary; elsewhere

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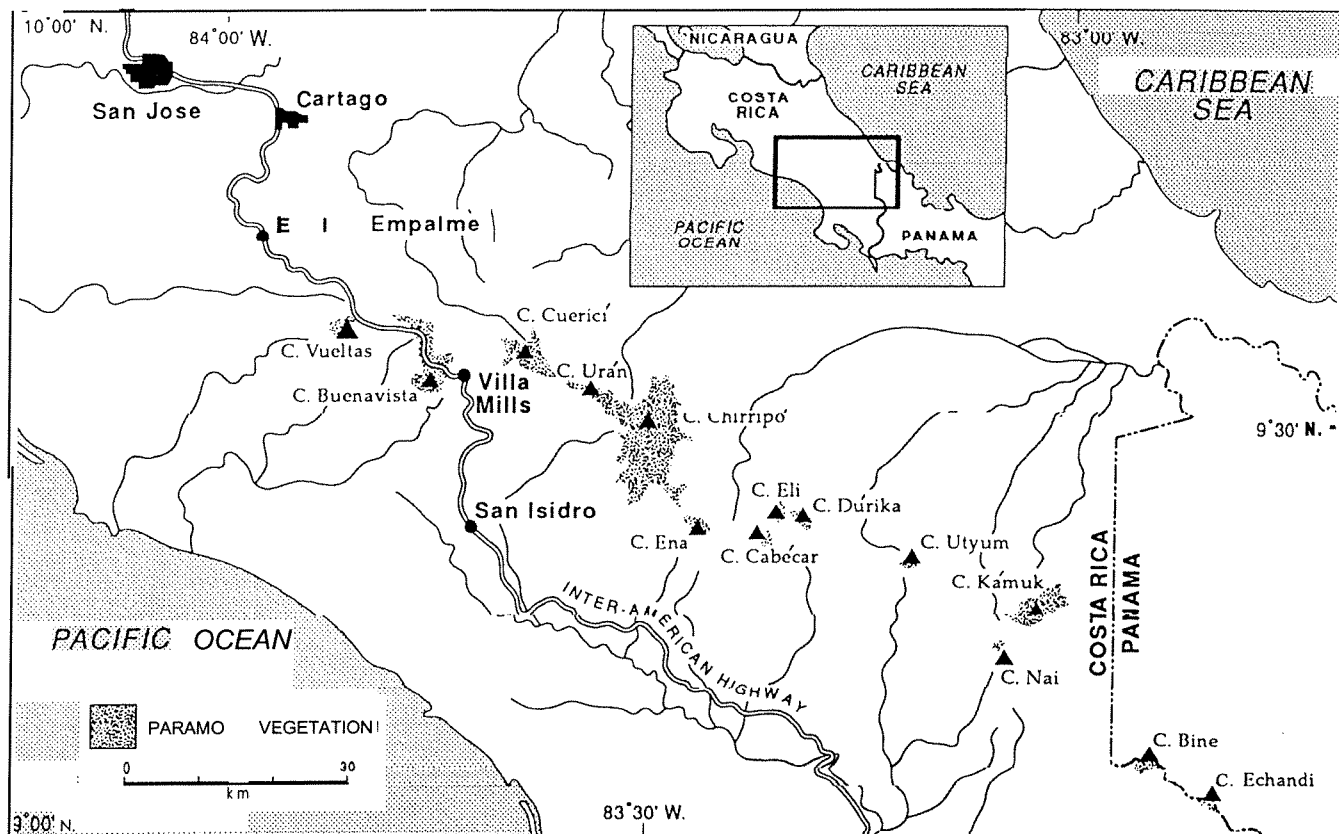


Figure 1. The páramos of the Cordillera de Talamanca, Costa Rica. The extent of páramo vegetation is based on Gómez (1986) and the 1:50,000 scale topographic maps published by the Instituto Geográfico Nacional.

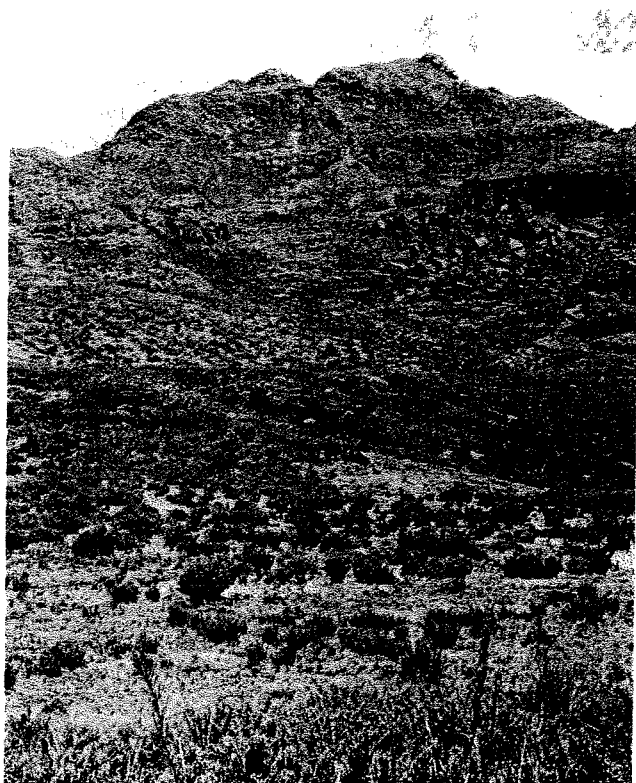


Figure 2. Nearly monospecific stand of the bamboo *Chusquea subtestata* in the Valle de los Concejos in the Chirripó páramo.

the two communities are separated by broad transitional zones supporting large shrubs and small trees other than oak. Some of the trees and shrubs within these transitional zones also occur, in more stunted form, within the páramos of the high peaks.

Low annual temperatures and a highly seasonal precipitation regime characterize the climate of the Costa Rican páramos. Meteorological data from the Cerro Páramo station (3475 m) near Cerro Buenavista show a mean annual temperature during the period 1971-79 of 7.6° C (Instituto Costarricense de Electricidad, unpub. data). The warmest months, April and May, averaged only 1.4° C warmer than the coldest month, January.

Average annual precipitation during the period 1971-1984 at Cerro Páramo was just over 2500 mm. Typically only about 10% of the total precipitation falls during the dry season or "verano" that lasts from mid-December to late April. Frost is frequent in the páramos, and hail has been observed (Dohrenwend 1972), but there are no reliable reports of snowfall (Coen 1983).

Clouds and mist frequently bathe the páramos, and must contribute an appreciable (though as yet unmeasured) amount of moisture. High atmospheric humidity moderates the dry season, but for days or weeks during this period the condensation belt lies below timberline, resulting in clear, dry

weather on the high peaks. Some perennial herbs die back at this time, and vegetation and litter quickly dry out, providing the fuel for fires.

Although burning is most widespread during the driest first 4 months of the year, a secondary rainfall minimum (the "veranillo") during mid-year may allow some burning. After a succession of several rainless days in July, 1981, experimental fires started in the Bucnavista páramo ignited readily and burned quickly to their fuel breaks (G.B. Williamson, pers. comm. 1982).

RECENT FIRE HISTORY

All of the Costa Rican páramos are protected within national parks or reserves, but there are no written fire records for these management areas. Documentary evidence of burning consists of occasional references in the scientific and popular literature, and old photographs that reveal evidence of burning. Fires are often too small to be readily apparent on satellite imagery, and aerial photograph coverage of the páramos is limited.

However, the slow rate of organic matter decomposition in the continuously cool páramo environment (Janzen 1973b) results in the long persistence of field evidence of past fires. Fire-killed shrub stems are conspicuous throughout the páramos, even at sites that burned more than two decades earlier. Some shrubs preserve evidence of multiple fires (fig. 3), and annual growth rings in living and fire-killed stems provide information on fire recurrence intervals (Horn 1986; Williamson and others 1986).

Field evidence indicates that all of the larger páramos east of Cerro Utyum (Dúrika, Chirripó, Urán, Cuericí, Buenavista, Vueltas; fig. 1) have burned since the mid-century (Weston 1981). Human carelessness, arson, helicopter and plane crashes, and escaped agricultural fires are among the ignition sources for recent burns (Horn 1986). Although human activity can explain all recent fires, lightning could also have played a role. Costa Rica has one of the highest incidences of thunderstorms in the world (World Meteorological Organization 1953, 1956), and lightning has been observed striking both the forested slopes and treeless summit of Cerro Chirripó (Horn 1989c). Such strikes might occasionally ignite fires on the high Talamancan peaks, as they do on Mountain Pine Ridge, Belize (Kellman 1975).

Many areas within the Chirripó and Bucnavista páramos have burned two or three times since 1950 (Horn 1986, 1989b, 1989c, 1990a). Fire recurrence intervals at specific sites have ranged from 6 to about 30 years. Given the slow rate of vegetation recovery within the páramos (see below), 6 years is probably close to the minimum fire recurrence interval possible. At least this many years of postfire growth is likely required to generate enough fuel to carry a second fire.



Figure 3. Resprouting shrub of *Vaccinium consanguineum* on Cerro Zacatales in the Bucnavista páramo showing stems killed in two successive fires. The larger, central stem was killed in the penultimate fire at the site, after which the shrub resprouted, producing the smaller dead stems that were killed by the last fire at the site. Following the last fire the shrub again resprouted. Older (twice-burned) stems can be differentiated based on position, degree of charring, presence or absence of bark, and extent of decay, and annual growth rings in dead and living stems can be counted to estimate fire recurrence intervals. The visible length of the tape measure is 60 cm.

Recent fires in the Chirripó páramo have been much larger than fires in the Bucnavista páramo. Páramo fires along the highway route have tended to burn out relatively quickly because they encountered insufficient fuel, fuel that was too moist, or a fire break created by a road or electrical transmission line corridor. The larger Chirripó páramo has provided an extensive and continuous fuel bed not interrupted by roads or other fire breaks, and fires, once started, have tended to spread over hundreds or thousands of hectares.

The post-1950 fire record in the Buenavista and Chirripó highlands suggests a link between fire and drought. Figure 4 graphs monthly precipitation in the driest month and the two consecutive driest months during the period 1952-1985 at Cerro Páramo (1971 onwards) and at the nearby Villa Mills station (3000 m) located just below timberline. I assume that these data reflect trends that would also have been evident at Cerro Chirripó, located 30 km to the east. The triangles denote known fire years in the Buenavista and Chirripó highlands, and in the intervening Cuericí páramo (fig. 1), with the size of the triangles indicating the total area above 3000 m elevation estimated to have burned in that year.

Not surprisingly, the largest high-elevation fires have tended to occur during the driest years. Between 1957, and 1985 there were 3 years in which the driest month (February or March) recorded less than 0.5 mm rainfall, and in each of those years a large (> 100 ha) fire occurred in the Chirripí páramo and surrounding montane forests. If rainfall records for 1952-1985 are indicative of long-term trends, the data suggest that extremely dry years conducive to widespread burning may be expected to occur about once a decade in the Chirripí and Buenavista páramos.

LONG-TERM FIRE HISTORY

Charcoal fragments in sediment cores from glacial lakes in the Chirripó highlands provide evidence of ancient fires in the Costa Rican páramos. A short (1.10 cm) sediment core recovered from Lago Chirripó (3520 m) in the Valle de los Lagos in 1985 preserved two distinct layers of macroscopic charcoal and an abundance of microscopic charcoal fragments (Horn 1989c). The charcoal particles appear to have been derived primarily from fires within the watershed of the lake and in adjacent areas of the Chirripí páramo. Charcoal concentrations varied with depth in the sediments, suggesting temporal variations in fire frequency (fig. 5). Although absolute fire frequencies cannot be determined from the charcoal data, variations in charcoal abundance may provide indications of relative fire frequencies. However, the relationship between fire history and sedimentary charcoal concentrations is complicated (Clark 1983), and factors unrelated to burning also may have affected the charcoal curve (Horn, 1989c).

Charcoal fragments were present in all of the samples from the Lago Chirripí sediment core, indicating that fires have affected the lake basin and surrounding areas since the sediments in the core began accumulating some 4000 years ago. A longer core raised from a glacial lake in an adjacent valley in 1989 (Horn 199017, and in prep.) spans the last 10,000 years, and also contains charcoal, confirming and extending the short core record. In the Chirripó páramo fire is clearly not a disturbance factor introduced by modern human society; burning due to human action or lighting has occurred for thousands of years.

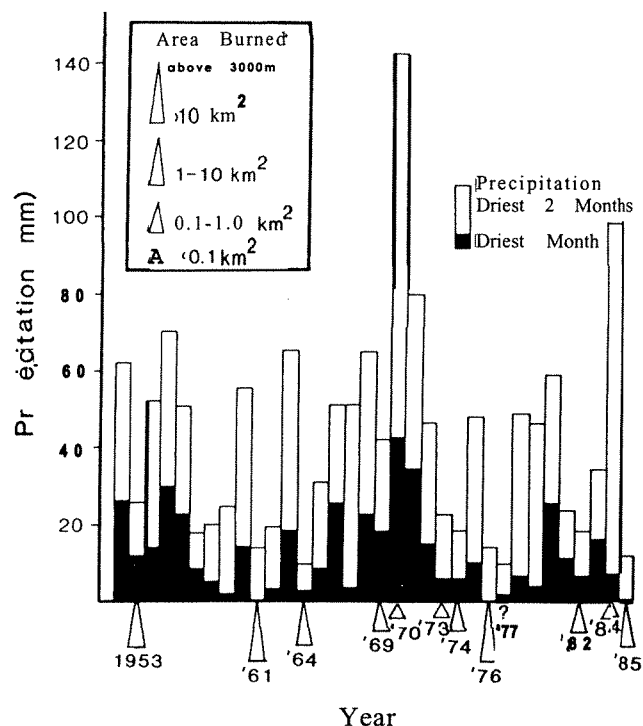


Figure 4. Dry season precipitation in the Buenavista highlands and the distribution of recent high elevation fires. Rainfall data are from the Cerro Páramo (1971 onwards) and Villa Mills stations (Instituto Costarricense de Electricidad unpub. data). The question mark in 1977 reflects uncertainty as to whether a forest fire that burned near Cerro Chirripó that year extended above 3000 m elevation.

THE IMPACT OF BURNING

Effects of Fire on Soils and Hydrology

Soils within the Costa Rican páramos are usually well-drained, rich in organic matter, and acidic, with pH values as low as 4.0 (Harris 1971). Soil samples collected by Leftwich (1973) within a recent burn area in the Buenavista páramo showed lower organic matter and C/N ratios, and higher exchangeable calcium and magnesium, than did samples from an adjacent unburned area. Field evidence of erosion has been noted on some burns, but soil loss following burning has not been quantified. No information is available on the hydrological impact of burning, though such studies would be of interest given the important watershed function of the páramos and surrounding montane forests.

Effects of Fire on Páramo Vegetation

Postfire vegetation dynamics in the Buenavista and Chirripó páramos have been examined by Janzen (1973b, 1983), Chaverri and others (1976, 1977, and in prep.), Williamson and others (1986) and Horn (1986, 1989b, 1990a). The slow rate of decomposition in the Costa Rican páramos has been an asset in these studies, as persistent fire killed stems can be identified and measured to provide information on the species composition and stature of the preburn woody vegetation.

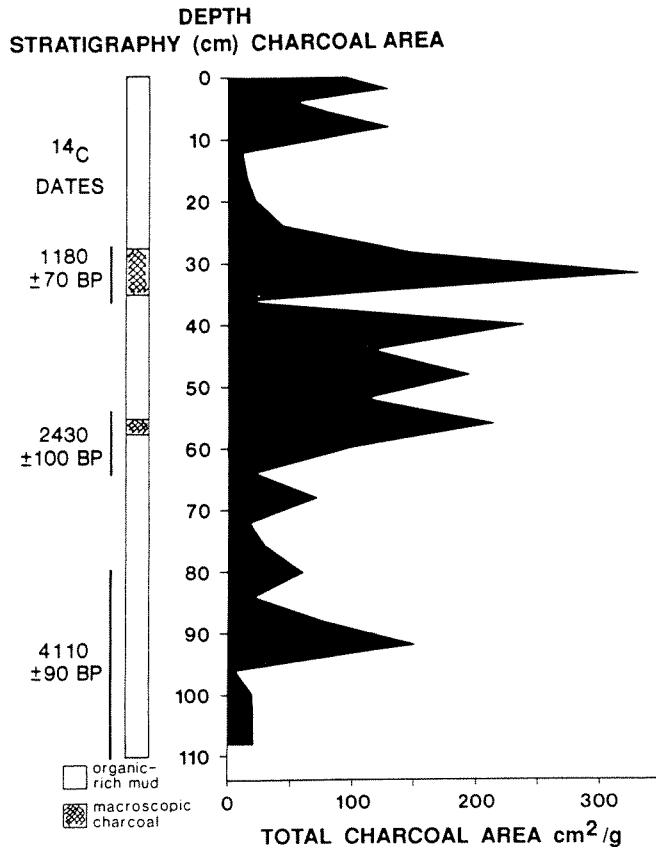


Figure 5. Diagram showing charcoal and sediment stratigraphy of a 110 cm core from Lago Chirripó.

Patterns of postfire vegetation recovery in the Costa Rican páramos support the initial floristics model of succession. The first species to colonize burned ground are the shrubs and herbs that comprise the mature vegetation. As appears to be the case in other tropical montane ecosystems (Smith and Young 1987), the Costa Rican páramos harbor no early successional specialists, and no invasion of plant species from outside communities takes place following disturbance.

Regeneration after and between fires is largely vegetative. Following fire, most woody plants and many herbs resprout vigorously, sometimes within just a few weeks of burning (Chaverri and others 1977). The bamboo *Chusquea subtessellata* and the ericaceous shrubs *Vaccinium consanguineum* and *Pernetia coriacea* show resprout rates of 90-100 percent following crown consumption and the death of aboveground stems (table 1). These vigorous sprouters rarely, if ever, establish seedlings, but may produce sprouts at new locations along widely diverging root and rhizome systems.

The common páramo shrub *Hypericum irazuense* supplements vegetative reproduction with seedling establishment. The species exhibited very low (4-14%) rates of basal resprouting at my study sites (table 1), but Janzen (1973b) noted abundant suckering by *H. irazuense* (his *H. caracasana*) following a fire on Cerro Asunción in the Buenavista páramo. Fire intensity and antecedent soil moisture conditions may be important controls of resprouting ability in this shrub.

For the narrow leaf congener *Hypericum strictum* all fires may be lethal; the species showed complete mortality at the Tower 65 site (table 1) and may be an obligate seeder.

Postfire seedling recruitment by *Hypericum* spp. and other shrubs and herbs relies largely on the influx of seeds from surrounding, unburned areas. The apparent lack of soil seed reserves (Horn 1989b) results in a very slow rate of seedling

Table 1. Percent basal resprouting by bamboo and shrubs following crown loss at paramo burn sites*.

	BURN SITE			
	Tower 65	Conejos	Zacatales	Sábila
<i>Chusquea subtessellata</i>	100	96	-	100
<i>Vaccinium consanguineum</i>	98	90	96	98
<i>Pernetia coriacea</i>	93	-	96	95
<i>Escallonia poasana</i>	-	-	-	57
<i>Rapanea pittieri</i>	25	-	-	15
<i>Hypericum irazuense</i>	4	6	12	14
<i>Senecio firmipes</i>	4	-	-	-
<i>Hypericum strictum</i>	0	-	-	-

*Only data for species with sample sizes greater than twenty at individual burn sites are included. For sample sizes and details on study sites and methods, see Horn (1989b).

Table 2. Postfire height and percent height recovery of resprouting shrubs and bamboo at paramo burn sites^a.

	SITE AND YEARS SINCE LAST FIRE			
	Tower 65 1 yr	Conejos 9 yr	Zacatales 12 yr	Sábila ≥ 12 yr
<i>Chusquea subtessellata</i>	34 cm (18%)	103 cm (98%)	141 cm (113%)	191 cm (129%)
<i>Vaccinium consanguineum</i>	22 cm (26%)	76 cm (71%)	67 cm (87%)	103 cm (88%)
<i>Pernetia coriacea</i>	16 cm (24%)		46 cm (97%)	65 cm (79%)
<i>Hypericum irazuense</i>	20 cm (15%)	91 cm (64%)	65 cm (71%)	111 cm (70%)
<i>Escallonia poasana</i>	14 cm (17%)		96 cm (116%)	148 cm (171%)
<i>Rapanea pittieri</i>	19 cm (14%)		117 cm (78%)	172 cm (126%)

^aOnly the six most common woody species are listed. See Horn (1989b) for samples sizes and standard deviations, and details on sites and field methods. Percentage height recovery equals mean maximum postfire plant height divided by the mean maximum height of unbroken, prefire (burned) stems. The prefire stature of plants partly reflects the time intervals between the last and penultimate fires at the sites, which was ≥16 years at the Tower 65 site, 15 years at the Conejos site, ≥ 12 years at the Zacatales site, and ≥29 years at the Sábila site.

colonization and may delay significant seedling recruitment for several years following fire. Where potential seed sources are distant (as near the centers of large burns), recolonization by *Hypericum irazuense* and other fire-sensitive species may not occur until the rare individuals that resprouted following burning grow to maturity and begin seed production within the burn area.

Growth rates of seedlings and suckers are extremely slow (tables 2,3). The fastest growing woody species, the bamboo *Chusquea subtessellata*, requires about 8-10 years to regain its average prefire stature (Janzen 1983; table 2, this paper). Coupled with the slow pace of seedling colonization, the slow growth rates within the Costa Rican páramos result in the long persistence of gaps created by burning. Bare patches of ground from 0.1 m² to 0.5 m² or larger in size may persist for a decade or more following fires, particularly on large burns where seed influx is low.

The strong resprouting ability of most of the dominant woody species in the Costa Rican páramos minimizes compositional shifts following burning (Horn 1989b). If a site dominated by bamboo and ericaceous shrubs burns, postfire cover the first year, and for at least a decade afterwards, will be dominated by bamboo and ericaceous shrubs. Major shifts in woody species composition will be observed only at sites with a substantial cover of fire-sensitive shrubs. Herbaceous species

may reach higher cover values on such burns, where greater shrub mortality results initially in less competition for space and other resources.

Based on observations at Cerro Zacatales in the Buenavista páramo, Williamson and others (1986) described a "fire cycle" in the Costa Rican páramos in which postburn cover is initially dominated by grasses and sedges, but reverts ultimately to shrub dominance if the site is kept free of fire for a sufficient period (perhaps 20 years). For reasons outlined above, such a cycle will be most evident where shrub mortality is very high, and where flowering plants are present nearby to reseed the burn site. When shrubs are closely spaced and suffer low mortality from fire, grasses and sedges may contribute little to postfire cover. Few graminoids or other herbs were present 3 years after a fire on Cerro Asunción (Janzen 1973b), a site characterized by high shrub survival and vigorous suckering. Greater herbaceous cover was observed 1 and 4 years after a fire at the nearby Tower 65 site, where 40% of the woody perennials (mostly *Hypericum irazuense* shrubs) died following crown loss. But even at this site, shrubs and bamboo dominated the initial postfire cover (Horn 1989b and unpub. data).

Graminoids, when abundant, will provide fine fuels that can support frequent fires. Williamson and others (1986) have suggested that when such fires occur at 5-10 year intervals

Table 3. Postfire stem diameters and percent diameter recovery for burned shrubs and bamboo at paramo burn sites^a.

	SITE AND YEARS SINCE LAST FIRE			
	Tower 65 1 yr	Conejos 9 yr	Zacatales 12 yr	Sábila ≥ 12 yr
<i>Chusquea subtessellata</i>	0.55 cm	0.73 cm	0.89 cm	1.20 cm
<i>Vaccinium consanguineum</i>	0.29 cm (13%)	1.98 cm (66%)	1.50 cm (70%)	2.13 cm (64%)
<i>Pernetia coriacea</i>	0.26 cm (26%)		0.68 cm (78%)	1.03 cm (63%)
<i>Hypericum irazuense</i>	0.16 cm (13%)	1.19 cm (58%)	0.86 cm (55%)	1.46 cm (60%)
<i>Escallonia poasana</i>			3.07 cm (125%)	3.52 cm (94%)
<i>Rapanea pittieri</i>	0.26 cm (15%)			2.92 cm (103%)

^aOnly the six most common woody species are listed. Sample sizes and standard deviations are listed in Horn (1986). Percentage diameter recovery equals mean maximum postfire stem diameter divided by the mean maximum prefire (burned) stem diameter. No data are available on prefire stem diameters of *Chusquea subtessellata*.

they may impede shrub recovery and facilitate the ultimate development of continuous grassland. Preliminary trials indicated that some shrubs may release allelopathic chemicals that inhibit the growth of grass and sedge seedlings and hence reduce the risk of fire (Williamson and others 1986).

CONCLUSION

Fire plays an important role in most of the world's shrublands (Christensen 1985), and the páramos of Costa Rica seem to be no exception. The low annual temperatures, high annual rainfall, and seasonal drought that characterize these tropical alpine habitats provide the fuel for periodic fires.

Sedimentary charcoal evidence shows that fires have occurred in the Chirripó páramo for at least 10,000 years; fires due to human activity or lightning may be of similar antiquity in other páramo areas.

Postfire regeneration follows initial floristics and is principally vegetative for the major woody species, many of which resprout vigorously after fire. The ultimate origin of this resprouting ability is uncertain, but selection in the face of periodic fires may have reinforced the trait. Some shrubs rely on seedling recruitment to repopulate burned areas, but the lack of soil seed reserves gives the sprouters a strong advantage in the first few postfire years. Low rates of seed influx and slow growth following germination or sprouting result in exceedingly slow recovery rates; 10 years after burning, most shrubs will not have regained their prefire adult stature and bare patches of ground may still be conspicuous.

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A SURVEY OF ABORIGINAL FIRE PATTERNS IN THE WESTERN DESERT OF AUSTRALIA

N.D. Burrows and P.E.S. Christensen¹

Abstract.—Aborigines who occupied vast tracts of the Australian deserts used fire extensively for many purposes. The recent departure of Aborigines from traditional burning practices has coincided with an alarming decline in native mammal fauna. It has been postulated that the combined effects of a changed fire regime, predation by feral animals, and competition from feral herbivores has contributed to mammal decline in this otherwise pristine environment.

Black-and-white aerial photography, satellite imagery, and field observations have revealed that the size, distribution, frequency, and intensity of fires in a part of the Western Desert have changed dramatically over the last 36 years. In an area west of Lake Mackay the average fire size has increased from 34 hectares in 1953 to over 32 000 hectares in 1986. The small-grained mosaic of burnt patches of varying ages that existed during Aboriginal occupation of the land has been obliterated by large, intense and infrequent lightning-caused wildfires. Some evidence of a relationship between fire mosaic and the richness of flora and fauna was obtained during this survey.

INTRODUCTION

About one third of the Australian continent is classified as desert. In the State of Western Australia, the Great Victoria, Gibson, and Great Sandy Deserts occupy some 1.3 million square kilometres and collectively are commonly known as the Western Desert (Tonkinson 1978). Rainfall is low (annual average ranges from 150 to 250 millimetres), and unpredictable, and long periods of drought are common. Rainfall is mostly from cyclones and thunderstorms and surface water is only abundant for short periods following rain. Summers are hot and winters are cool. The Western Desert is well vegetated and surprisingly rich in wildlife. Highly flammable hummock grasslands, comprising species of *Triodia* and *Plectrachne* (spinifex), dominate red sandy soils.

Aborigines first arrived on the Australian continent at least 50,000-60,000 years ago and occupied the deserts of the interior by at least 30,000 years ago (Mulvancy 1975; Flood 1983). Aboriginal people showed remarkable resilience and resourcefulness to survive in a vast expanse of scattered food and water resources (Tonkinson 1978). They were highly mobile, were able to exploit a variety of resources in different areas at different times, and developed a detailed knowledge of the environment. Fossil evidence suggests climatic and cultural continuities lasting at least 10,000 years (Gould 1971), so there has been a long period of Aboriginal influence on the desert biota.

The Western Australian Department of Conservation and Land Management (CALM) manages about ten million hectares of desert conservation reserves which range in area from two hundred thousand hectares to two million hectares.

The management priority for these reserves is the conservation of native flora and fauna. However, in spite of the apparent pristine nature of these reserves and the lack of direct European impact, a sudden and alarming decline in native mammals has been reported (Bolton and Latz 1978; Burbidge 1985; Burbidge and others 1988; Burbidge and McKenzie 1989). Burbidge and Jenkins (1984) reported that about 33 percent of Western Australian desert mammals are extinct or endangered. They noted that this decline had occurred over the last 30 to 50 years. Burbidge and McKenzie (1989) have shown that all declines and extinctions have been restricted to native mammals with a mean adult body weight in the range from 35 grams to 5,500 grams (critical weight range). The desert conservation reserves are relatively pristine and have not been directly modified or disturbed by European activities. Generally, recent extinctions of wildlife have been associated with habitat destruction or modification by humans (Burbidge 1985).

Ngaanyatjarra Aborigines from the Warburton area of Western Australia believe that the "mitika", or burrowing bettong (*Peromyscus lesueur*), had "gone to the sky because the country had not been cleaned up" (de Graaff 1976). "Clean up" is a term often used by Aborigines for burning the vegetation (Jones 1980). Kimber (1983) reported that Pinlubi Aborigines believed that perhaps a "big bushfire" caused the disappearance of the golden bandicoot (*Isodon auratus*). Scientists have proposed three main hypotheses to explain the decline and in some cases, extinction of desert mammals. Burbidge and Johnson (1983) proposed that changes in fire regime, predation by feral animals, and competition from feral herbivores as the main factors, acting either independently or in combination, leading to mammal decline in the arid zone.

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Recent changes in the fire regime were a direct consequence of the exodus of Aboriginal people from the desert to settlements in missions, outstations and other communities (Could 1971; de Graaf 1976; Latz and Griffin 1978; Kimber 1983; Saxon 1983). Latz and Griffin (1978) postulated that Aborigines created a stable ecosystem by "burning the country in a mosaic pattern". They claimed that mosaic burning reduced the extent and continuity of heavy fuels, and therefore reduced the occurrence of intense wildfires. They also stated that a second effect of mosaic burning was to create 3 range of "states" in the vegetation, from early postfire plant communities to old mature patches. They were of the opinion that such diversity of states would host a greater variety of plants and animals.

The extensive use of fire by desert Aborigines is well documented by early explorers (Warburton 1875; Carnegie 1898) and more recently by anthropologists and ecologists (Finlayson 1943; Jones 1969; Calaby 1971; Gould 1971; de Graaf 1976; Tonkinson 1978; Kimber 1983). Kimber (1983) observed that the Pintubi used fire in a skilful and controlled manner for many reasons, such as hunting, signalling, to "clean up" the country, for ceremonies, and for fun. He provides a general description of when fires were lit and the range in fire sizes. He also made some rough calculations of the proportion of country burnt and the approximate age since fire, based on information in the diaries of Davidson, who explored parts of the Tanami Desert in 1900. However, little quantitative information about the fire regime during traditional Aboriginal occupation of vast tracts of desert land is available.

Quantitative data on past and present fire regimes are of considerable interest to the Western Australian Department of Conservation and Land Management, which is engaged in a multidisciplinary study aimed at maintaining and improving the conservation status of desert ecosystems. As part of this project, experimental reintroductions of selected species of rare and endangered mammals to the Gibson Desert Nature Reserve will be attempted. Prior to reintroduction, prescribed fires will be used to recreate the kind of fire mosaic which is believed to have existed before the departure of Aborigines. Feral predators such as foxes and cats will also be controlled in the experiment.

The aim of this study is to define, as clearly as possible, the fire regime during the occupation of the Western Desert by Aborigines prior to European contact and to compare this with the present-day fire regime. In doing so, we could test the hypothesis of a recent and dramatically changed fire regime as proposed by Latz and Griffin (1978) and others. A knowledge of past fire regime would also greatly assist with the development of appropriate fire management strategies for desert conservation reserves.

We use Gill's (1981) definition of fire regime, which is the history of fire frequency, fire season (season in which fires burnt), fire intensity, and fire size.

METHODS

The departure of Aborigines from their desert homelands started with first European contact at the end of the nineteenth century. Amadio and Kimber (1988) present a summary of European exploration and contact with Aborigines of the northern portion of the Western Desert and also describe the movements of Aboriginal people away from their homelands and into European settlements. To reconstruct the fire regime, it was desirable to study fire on land from which Aboriginal people living a more-or-less traditional lifestyle, had most recently departed. We learnt that a very remote tract of land to the west of Lake Mackay, in Western Australia was probably the last homeland utilized in a traditional manner by Pintubi people (Richard Kimber pers.comm.). The study site of some 54,000 hectares is on the eastern edge of the Great Sandy and Gibson Deserts and lies between longitudes 128°35'E and 128°50'E and latitudes 22°8'S and 22°18'S (Figure 1). The area is arid, with an average annual rainfall

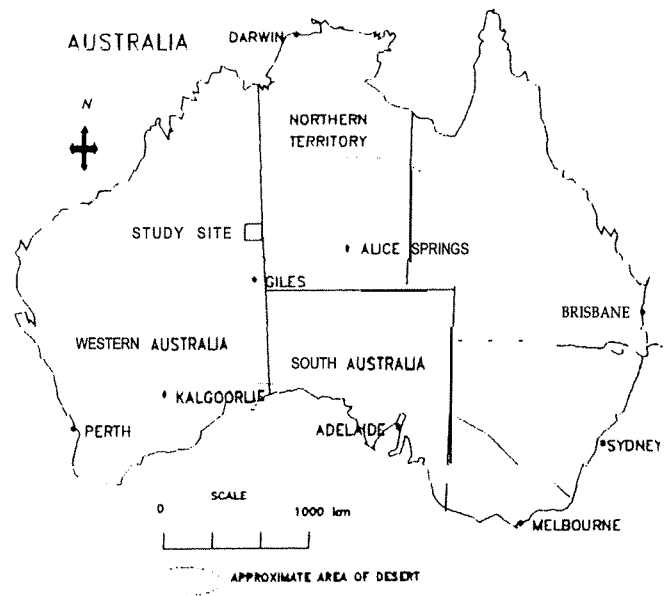


Figure 1: Location of the study area in the Western Desert. The approximate boundary of land classified as desert is shown.

probably less than 225 mm (there are no meteorological stations nearby). Most of the rain falls in summer but both the amount and the seasonal distribution are highly variable. As a result of the arid climate and sandy soils, the vegetation consists mainly of hummock grasses (*spinifex*) and associated small shrubs, herbaceous plants and scattered low trees. The sand plain that covers most of the study area is crossed by

longitudinal, stable dunes which trend east-west. There are numerous salt pans, salt lakes, and clay pans scattered throughout the area. The largest salt lake is Lake Mackay, which has a total area of about 3,500 square kilometres (Blake 1977). The salt lakes, salt pans, and clay pans are dry except after heavy rain.

The main exodus of Pintubi Aborigines from this area commenced in the early 1960s, with the last people coming into Kintore and Kiwirrikura communities in 1985 (Richard Kimber, pers. comm.).

We have used early black-and-white aerial photographs to help reconstruct the fire regime at the study site during Aboriginal occupation. This technique was supplemented by reviewing the literature and by talking with Pintubi and Pitjantjatjarra Aborigines to obtain information about their use of fire. The current fire regime, particularly size and distribution of burnt patches, was inferred from Landsat satellite imagery and by visiting the study site and surveying fire history. While in the field we also surveyed vascular **plant** and vertebrate **animal abundance** within areas of different age since the last fire.

Aerial Photographs and Landsat Imagery.

Details of aerial photography available for this area are presented in table 1. The earliest aerial photographic surveys were completed in 1953 by the Royal Australian Air Force as part of the Blue Streak rocket project during an era of extensive rocket development and testing in Australia. Fire scars showed clearly on both aerial photographs and Landsat imagery. Fire scars that appeared on the 1953 photography were mapped onto a base map at a scale of 1:50,000.

Additional fire scars which appeared on successive photographs were mapped onto separate sheets, but at the same scale, to form a series of overlays. Landscape features such as salt lakes, clay pans, salt pans, sand dunes, and major creeks and streams were also mapped. The area and perimeter of each fire scar for each time series was calculated using a computer-linked digitizing board. Initially, an attempt was made to accurately age fire scars based on tonal intensities of the scars indicated on the photographs. The different toning of the fire scars represented different stages of revegetation, or

fire succession, with recently burnt areas showing up as very bright patches. This proved to be difficult and fire scars could only be rated as "very recent" (up to 5 years old), or "recent" (5-10 years old), based on the extent of re-vegetation. While older scars were barely discernible, no attempt was made to map scars that did not have clearly visible boundaries.

Field Survey of Biological Indicators

The second technique used to obtain details about past and present fire regimes and the fire environment of the study area was ground survey of biological indicators. Some 50 kilometres of line transect was surveyed by vehicle traverse in 1989 and visually discernible fire boundaries recorded. A fire boundary was defined as the boundary between two recognizable fuel ages or between vegetation burnt at different times. Within each fuel age encountered, the time since the last fire was estimated by counting "annual" growth rings from tree stem cross-sections. Because of the uncertainty of the period between growth rings, accurate aging of fire scars was not possible. Based on ring counts from areas of known fire history, stem analysis enabled the time since fire to be estimated to within ± 11 percent of actual time. Measures of vegetation cover and height were also useful for estimating the age of vegetation. In some instances, the aerial photographs were used to estimate time since last fire. Circular plots of 100 metres radius were established in each fuel age and the number and abundance of plant species recorded. A list of animals utilizing each fuel age was compiled by searching for burrows, diggings, scats, and tracks. The Pintubi and Pitjantjatjarra guides who accompanied us, skillfully identified signs of animal activity and provided us with the Aboriginal names for the animals.

RESULTS

Aerial Photographs

There has been a dramatic change in the mean and median size of burnt patches in the period from 1953 to 1986. From table 1, it can be seen that the area recently burnt (up to 10 years prior to photography) has increased from 23.6 percent of the study area in 1953, to almost 60 percent by 1986. Also, the mean size of fires has increased almost 1,000 fold

Table 1. Number, area, and perimeter statistics for burnt patches clearly visible on black-and-white aerial photography and on Landsat satellite imagery of a 53,483 ha study in the Western Desert, Western Australia.

Year	Number of burnt patches	Burnt patch size (ha)				Total burnt (ha)	Total perimeter (km)
		Maximum	Mean	Mode	Median		
1953	372	1,744	34	2	6	12,643	1,198
1973	27	13,534	845	5	197	22,800	412
1977	3	30,618	10,584	.	.	31,752	293
1988	1	32,184	.	.	.	32,184	272

over the same period. Habitat boundary, which is the total fire perimeter within the study site and is a measure of the boundary between vegetation of different ages since fire, has decreased from 1,198 kilometres in 1953 to 272 kilometres in 1986. This indicates a substantial reduction in the diversity of fire ages or states of postfire succession within the landscape.

A visual inspection of the fire scars mapped for each time of photography revealed a number of obvious patterns. In 1953, when groups of Pintuhi Aborigines were living on the land, there were some 372 individual, recent fire scars visible on the aerial photographs (see fig. 2). Many of these concentrated around major salt lakes, claypans, and salt pans. While it is not possible to determine the ignition source of all fires, many scars showed the classic shape of having been lit

by a person dragging a firestick in a straight line. Many of the fires burnt between the sparsely vegetated sand dune crests. By 1973, some 11 years after Aborigines began to leave the land, the small-grained mosaic of burnt patches that existed in 1953, had begun to be erased and to be replaced by large tracts of recently burnt country and large tracts long unburnt. The ignition source of these fires may have been lightning or the few Aboriginal people who remained in the area. This temporal trend of increasing fire size and increasing pyric homogeneity has continued until the present day, and there now exists vast tracts of country burnt at the same time by a single fire or multiple lightning strikes. There are also vast areas which have not been burnt for in excess of 30 years. This pattern is repeated across the Western and Central Deserts (Griffin and Allan 1985).

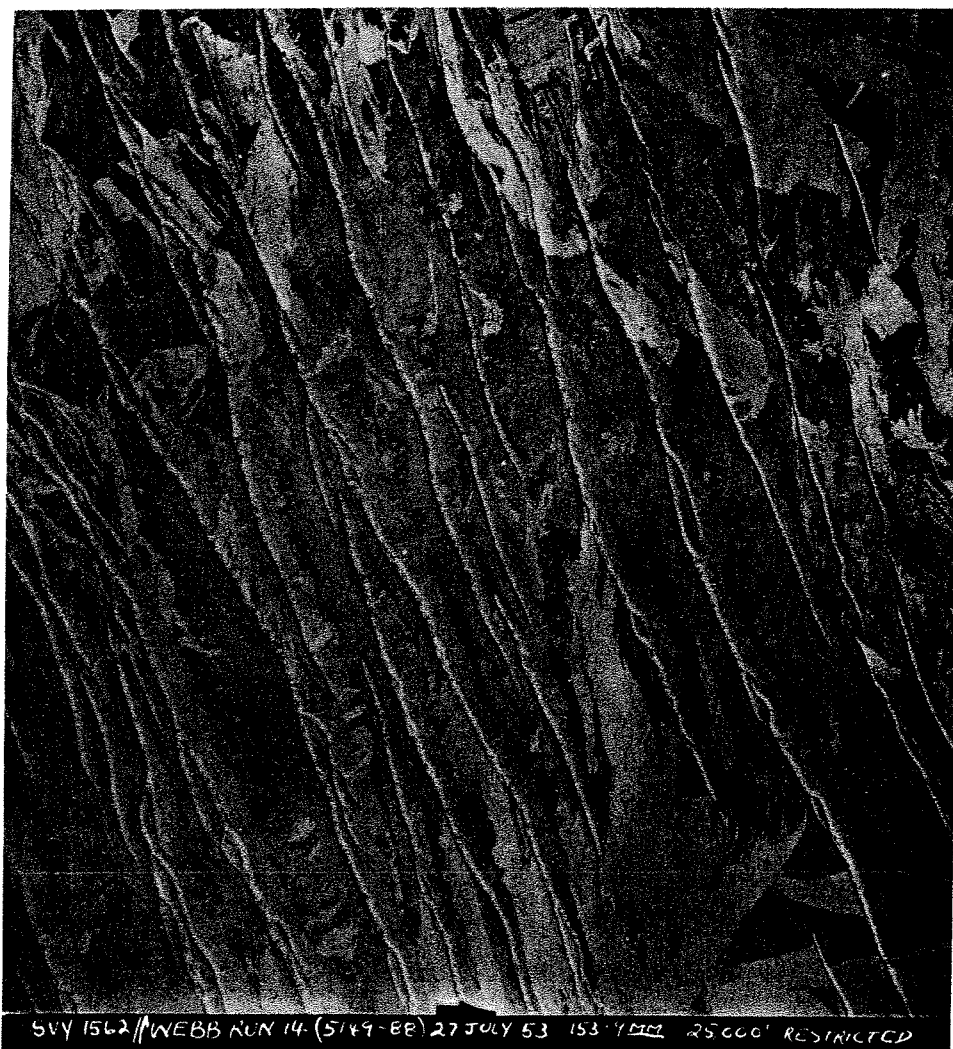


Figure 2. The patchwork of fire scars is clearly evident on early (1953) black-and-white aerial photographs. Most fires were lit by Pintuhi Aborigines who occupied the desert at the time of photography.

The frequency distribution by size class of fire scars is shown in figure 3 for 1953 and 1973 photography. By 1977 and 1986, most of the study area had been burnt by only a few fires lit at about the same time.

A useful measure of the size and distribution of burnt and unburnt patches is the ratio of variance to mean patch size (Peilou 1977). A random distribution produces a ratio of near 1. A uniform or over dispersed distribution results in a ratio greater than 1 while a clumped or contiguous distribution yields a value much less than 1. In 1953, the patchiness ratio of both burnt and unburnt areas was 0.62 to 0.72, or close to 1, indicating a random distribution of patches (figure 4). The mean length of continuous burnt vegetation had increased from 467 metres in 1953 to 2,570 meters in 1986 and the variance ratio had reduced to 0.43, indicating a clumped distribution of patch size and a significant increase in mosaic grain size (Peilou 1977). Line transects across photographs of a portion of the study area to reveal a spectrum of recently burnt (< 10 years) and long unburnt vegetation are also useful for quantifying burn mosaics. This "substitute pattern" of alternating black and white stripes is a representation of the varying grain size of the two phase mosaic (Peilou, 1978). These patterns are presented in figure 5 for the 1953 photography and 1986 satellite imagery.

Field Survey of Biological Indicators

An example of the results of a vehicle traverse along a line transect showing the ages of vegetation since the last fire and the total number of animal species recorded from observations of tracks, diggings, and scats is shown in figure 6. The traverse was conducted in 1989. While most of the vegetation, was about 6 years old at the time of the traverse, there were small patches of older vegetation which had escaped the most recent fire. Often, these patches were found on the leeward side of natural fire barriers such as sand dune

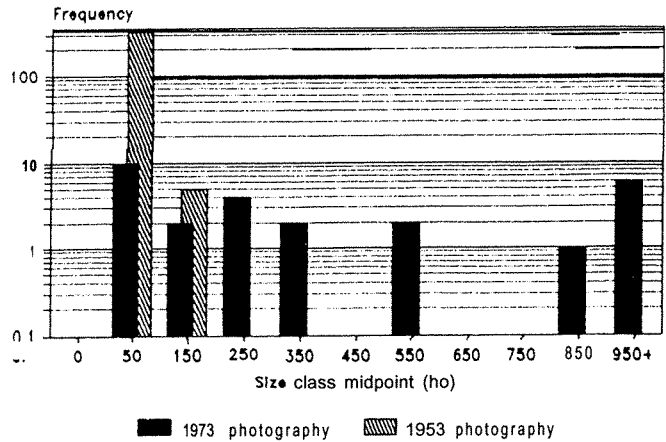


Figure 3. Frequency distribution of size classes of recent fire scars evident on 1953 and 1973 black-and-white aerial photographs of a part of the Western Desert.

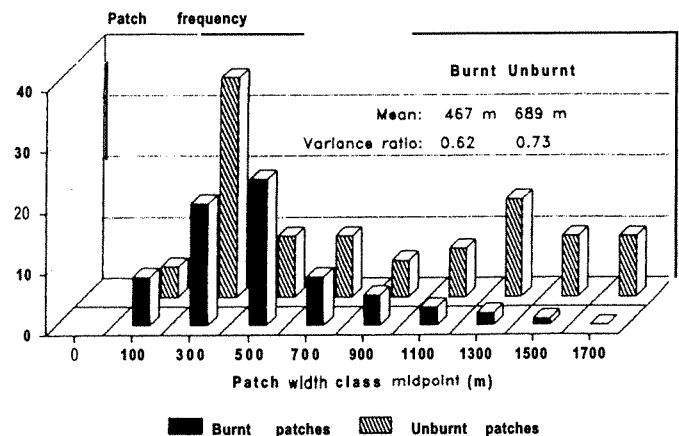


Figure 4. Percentage frequency distribution by size classes of the width of recently burnt (< 10 years) and long-unburnt patches of desert vegetation measured along transects across 1953 black-and-white aerial photographs.

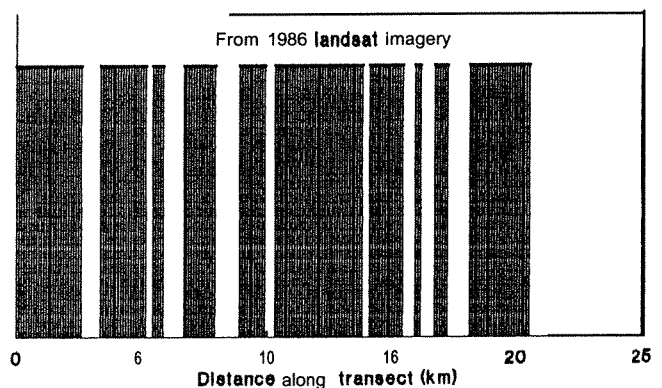
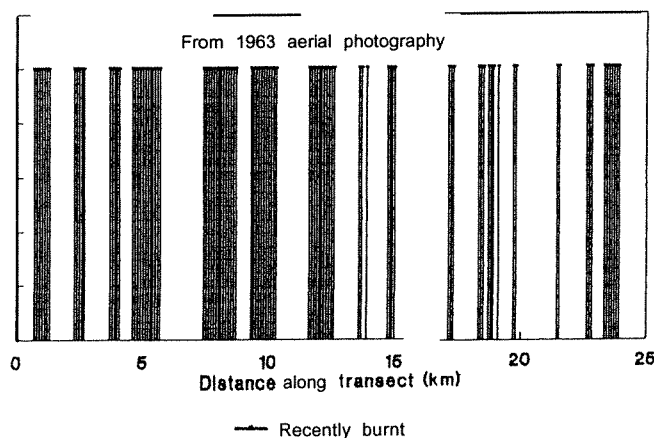


Figure 5. Substitute patterns for two two-phase mosaics (recently burnt and long-unburnt vegetation) of the Western Desert study area from 1953 aerial photography and 1986 satellite imagery.

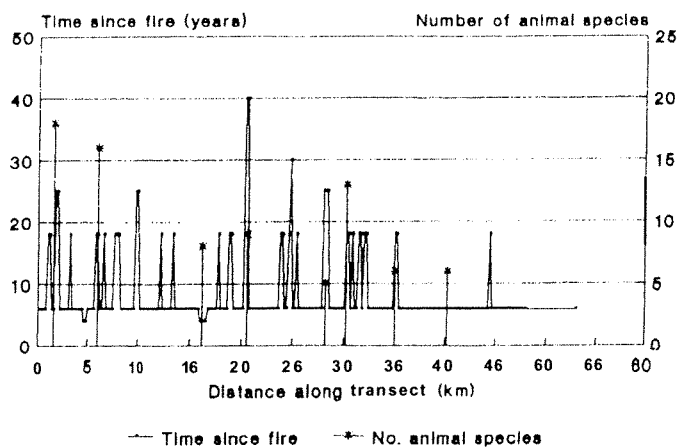


Figure 6 Age of vegetation (time since fire) along a transect across desert vegetation in 1989. Also shown are numbers of animal species estimated from diggings, scats, and tracks at points along the transect.

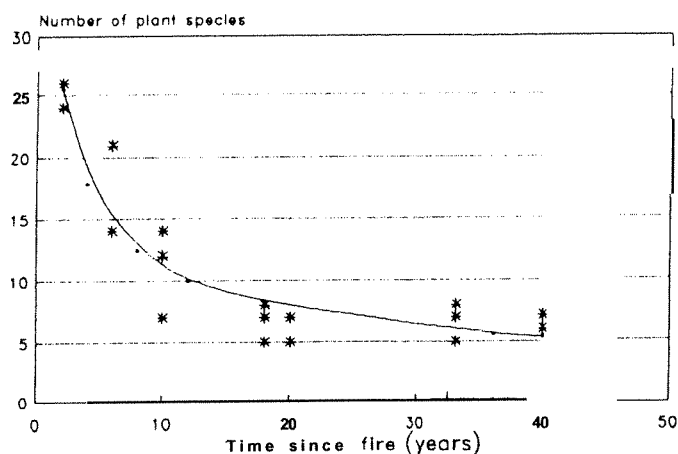


Figure 7. Numbers of plant species within a 100-meter-radius plot with time since last fire in desert vegetation near Lake Mackay, Western Australia.

crests, salt lakes, and claypans. Generally, long unburnt patches were small (200–400 m across). The oldest patch of vegetation was 40 ± 4 years. Animal species numbers, based on the survey technique used here, were highest in areas where there was a mosaic of 6- and 15-year-old vegetation. Where vegetation age was predominantly 6 years or less, or in one case where it was 40 years old, species numbers were low.

Plant species diversity decreased with increasing time since fire (fig. 7). Older vegetation was dominated by large, senescent rings of spinifex (*Triodia* species), whereas recently burnt patches contained a range of herbaceous plants as well as woody shrubs and spinifex. Many woody shrubs had resprouted from lignotuber or regenerated from soil-stored seed following fire.

DISCUSSION

Fire size

There has been a dramatic and sudden increase in the mean and median size of burnt patches in the study area, coinciding with the departure of Pintubi Aborigines. The average size of a burnt patch has increased from 34 hectares in 1953 to 32,184 hectares in 1986 (table 1). During Aboriginal occupation of this land, there existed a fine-grained mosaic of burnt patches across the landscape as a result of Aboriginal burning and natural lightning fires. The Pintubi and Pitjantjatjarra men who guided us around the study area, found old, long-unburnt spinifex as aesthetically displeasing and continually fired the spinifex as we travelled across the desert.

Kimber (1983) suggests that Aborigines had a good deal of control over fire, using wind, humidity and natural fire barriers such as claypans and sand dunes to control the size and intensity of fires. Our observations of the concentration of fire scars around resource-rich areas such as rockholes, creeks, claypans, and salt lakes is consistent with observations made by Kimber (1983). The fire regime around these resource rich landscape units may not be typical of areas less utilized by Aborigines. Partitioning and utilization of the landscape by Aborigines requires further investigation.

The abundance of small fire scars (< 10 hectares) visible on the 1953 aerial photography suggests either fires were lit under mild conditions and burnt at a low intensity or extensive tracts of heavy fuel sufficient to sustain large and intense fires did not exist. Many generations of Aborigines frequently burning off the land would result in a situation of discontinuous, patchy fuels, ranging from recently burnt to long-unburnt patches. However, when the human ignition source was removed from the desert, the fuels gradually accumulated over large, continuous tracts of land. Lightning strikes in summer have resulted in the massive and intense wildfires observed today. The grain size of the two-phase mosaic (recently burnt and long-unburnt) has increased over the last 36 years, as shown in figures 4 and 5.

Time of Year of Fires

Kimber (1983) believes that most burning by Aborigines was done in August to October and immediately prior to rains in December to February. Occasionally, large fires caused either by Aborigines or by lightning, burnt during the hot, dry, windy summer months. In the area studied here, it would not have been possible for a fire to become very large in 1953, as the fuels were discontinuous as a result of patch burning and natural fire barriers. Kimber suggests that the time of year for burning is not as important to Aboriginal people as the opportunity to burn. de Graaf (1976) observed that Aboriginal fires in the desert were lit all year round and not seasonally.

Both de Graaf (1976) and Kimber (1983) reported that certain areas of the desert were not burnt by Aborigines because Aborigines did not visit these places for religious reasons, or feared that fire would destroy sacred objects. The season of burning was, however, very important in the monsoon forest regions of the Northern Territory (Jones 1980; Haynes 1985) and to Wadjuk Aborigines in the south-west of Western Australia (Hallam 1975).

Today the main ignition source in the remote deserts is lightning. Thunderstorms are common over the summer months and large, lightning-caused wildfires have been reported (Griffin and others 1983).

The benefits to Aborigines by way of increased food resources as a result of firing the spinifex were evident during this study. Recently burnt country supported a diverse range of herbs and animals, particularly reptiles, whereas long-unburnt vegetation was generally less diverse in flora and fauna. However, we were unable to show any strong correlations between time since fire (fuel age) and total animal species numbers, although there was a trend between the spatial diversity of fuel age and animal numbers (fig. 6). Animal species numbers were based on visual observations of tracks, diggings, and scats, thus limiting the extent to which the data can be interpreted. More detailed studies of animal activity in relation to the temporal and spatial diversity of fuel age are needed. Postfire succession in spinifex communities has been described by Burbidge (1943) and Suijndorp (1981). All authors report an increased level of plant diversity soon after fire. The range of fire-adaptive traits expressed by desert vegetation has also been reported by these authors.

As noted, there has been a significant change in fire regimes in recent times, and there is at least limited scientific evidence to suggest that this has contributed to the decline in mammal fauna. This change may have further predisposed mammals to predation by introduced predators. It is reasonable to accept the importance of temporal and spatial diversity within a landscape on resource levels and habitat opportunities (Latz and Griffin 1978, Pielou 1977). Saxon (1984) stated that "when large areas of a single landscape type are subjected to large uniform disturbances, they threaten the survival of wildlife species which depend on irregular boundaries of natural fire patterns to provide a fine grained mosaic of resources". Bolton and Latz (1978) have shown that a range of post-fire successional stages is important habitat for the western hare-wallaby (*Largorhynchus hirsutus*). Burbidge and Pearson (1989) explain the lack of rufous hare-wallabies (*Largorhynchus hirsutus*) in the Great Sandy Deserts as being due to the lack of frequency of small-scale burns and to high fox numbers.

It is somewhat ironic that modern mammal extinctions in the Australian deserts are in part due to the changed fire regime that resulted from the departure of Aborigines and consequent lack of Aboriginal burning. Tindale (1959), Merrilees (1968), and Jones (1968) have all concluded that extensive burning by Aborigines contributed to the extinction of the Pleistocene mega-fauna. Today, it is likely that the large, intense wildfires which occur throughout the deserts are placing extreme stress on some plant and animal communities (Griffin 1981). These intense fires are damaging vast areas of fire-sensitive vegetation such as marble gum (*Eucalyptus gongliocarpa*), desert oak (*Allocasuarina decaisneana*), and mulga (*Acacia anuera*) (Start 1986). There is sufficient evidence of the disadvantages of the current wildfire regime on the conservation status of desert reserves to warrant the development and implementation of managed fire regimes that mimic those in place during Aboriginal occupation of the land.

Today, aircraft are being used in parts of some Western Australian desert conservation reserves to set patch burns under carefully defined conditions to create a mosaic effect of burnt and unburnt patches across the landscape (Burrows and Thomson 1990). This study, together with detailed fire ecology studies currently in progress, will provide a basis for determining the frequency of fire and the size and distribution of burnt patches.

When the habitat has been rehabilitated through the prescribed use of fire and introduced predators controlled, then there will be an opportunity for translocating rare and endangered mammals to parts of their former range.

CONCLUSION

Black-and-white aerial photographs, Landsat imagery, and field observations have revealed that the size and intensity of fires in a part of the Western Desert west of Lake Mackay have increased dramatically over the last 36 years or so. This increase is attributed to the departure of Aboriginal people from the area during the 1960s. Aborigines used fire extensively for a multitude of reasons, resulting in a small-grained mosaic of burnt patches of different ages across the landscape. Such landscape diversity maximised resources available to Aborigines and to desert animals. Today, in the absence of frequent burning by Aborigines, fuels have accumulated over vast areas and when these fuels are ignited by lightning under hot, dry, windy summer conditions, large and intense wildfires sweep across the desert. This changed fire regime appears to have resulted in a lower diversity of animals and plants.

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INDIAN USE OF FIRE AND LAND CLEARANCE IN THE SOUTHERN APPALACHIANS

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Abstract—The myth of an unbroken primeval forest, extending across eastern North America at the dawn of European settlement, has been perpetuated in the writings of both laymen and scholars throughout the present century. Accounts of sixteenth, seventeenth, and eighteenth century explorers, however, document vast amounts of cleared land held by aboriginal inhabitants, who likely populated the continent in much higher numbers than have been traditionally accepted. Fire was the principal tool used by the Indians to clear vegetation. Despite frequent historical reference to the Indian use of fire and the documentation of Indian old fields, the role of fire has been largely underplayed. Fire was implemented for forest management, driving game, and preparing land for agriculture. This paper examines the impact of fire and related anthropogenic disturbances on the southern Appalachian landscape before white settlement.

INTRODUCTION

Man's role as an agent of landscape change has long been a theme of research in historical geography (Newcomb 1969). However, the influence of eastern North America's aboriginal inhabitants on the physical environment before European settlement has not been studied adequately. This paper offers an overview of anthropogenic disturbances in the southern Appalachians during an era of aboriginal habitation, with especial reference to population, fire, land use, and land clearance.

ACCOUNTS BY EARLY EUROPEAN EXPLORERS

Permanent European settlement of the eastern United States did not occur until more than a century after the Columbus landfall in 1491, despite explorers' ventures along the coast, and subsequently into the interior of the continent, in pursuit of geographic knowledge during the sixteenth century (Brown 1948). Journals often contain comments as to the apparent presence or absence of forest, but other landscape traits were documented as well, such as aboriginal population and land use. In any event, the early explorers have provided documentation that refutes the popular notion of an unbroken virgin forest extending across eastern North America. Of particular significance were the travels of Giovanni Verrazano in 1524, Jacques Cartier a decade later, and Samuel de Champlain in the early 1600s (Sauer 1971, 1980), but their accounts depict extensive areas of cleared land prior to European settlement only along the Atlantic coast and adjacent navigable waterways. Very few reports documenting conditions of the southeastern interior were provided by explorers. Narratives of the expedition led by Hernando de Soto between the years 1538 and 1543, however, offer illustrations of extensive maize fields, canebrakes, and open land on the southeastern coastal plain and in the southern mountains (Boume 1904; Hakluyt 1611; Rostlund 1957; U.S. 1939).

ABORIGINAL POPULATION AND DEPOPULATION

Supplementing explorers' accounts is a body of literature in which students have sought to determine the pre-contact aboriginal population of the Americas. These studies suggest that the aboriginal population of the southern Appalachians was much greater than heretofore accepted, and that it declined rapidly, largely because of disease transmitted by the Europeans following the Columbus landfall in 1492. Furthermore, aboriginal inhabitants were numerous enough and sufficiently advanced to significantly alter the region's vegetation.

Humans have occupied the southern Appalachians for over 12,000 years (Dickens 1976; Frizzell 1987). It is widely accepted that the Cherokees occupied the region at least since the protohistoric period; their settlement core was restricted to western North Carolina, east Tennessee, north Georgia, and northwestern South Carolina, but claimed lands extending north to West Virginia and Kentucky (Dickens 1987; Frizzell 1987; Goodwin 1977). Mooney estimated the Cherokee population at no more than 22,000, a figure accepted and advanced by Kroeber (Denevan 1976; Goodwin 1977; Kroeber 1939; Swanton 1946).

Denevan, however, has indicated that the "authority of Kroeber has impeded serious consideration of North American aboriginal populations" and that "it is time for a reconsideration" (Denevan 1976). Unfortunately, one of the principal problems in estimating North American aboriginal populations, especially in the southeastern interior, is the lack of historical evidence. Historical documentation regarding Indian populations is more widely available for Latin American regions than for Anglo-America, largely because the former have a longer history of direct European contact and settlement. Because "estimates of aboriginal American populations have yielded a picture of small scale preconquest human population in the Western Hemisphere" (Dobyns 1966; Denevan 1976), anthropologist Henry Dobyns has proposed the use of depopulation ratios for calculating pre-Columbian

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populations. His estimates contrast rather sharply with Kroeber's; for example, Kroeber estimated a hemispheric total of 8.40 million, whereas Dobyns estimates 90.04-112.55 million (Denevan 1976), and Geographer Michael Williams has noted:

There is the strong possibility that in the late fifteenth century the Western Hemisphere may have had a greater total population than western Europe. The implications of these figures for forest disturbance and destruction are enormous (Williams 1989).

Today, Kroeber's estimates are considered much too low (Denevan 1976), and Dobyns' method offers an alternative, probably more realistic estimate. Dobyns' scheme employs a depopulation ratio, that is "the ratio of degree of decline from the time of contact to the population nadir" (Denevan 1976). Dobyns determined the depopulation ratios for aboriginal tribes and regions for which relatively reliable information is available and derived an average of 20:1 (a population decline of 95%). Borah further supports high figures; he estimated pre-contact New World native population at about 100 million, which suggests a depopulation ratio of up to 25:1 (Borah 1964; Denevan 1976; Dobyns 1966).

The application of depopulation ratios is a viable means of estimating the pre-contact aboriginal population of the southern Appalachians. Archaeological evidence and travel accounts indicate rapid population decline during the sixteenth century, and the southeastern interior was not subject to exploration, description and interpretation, and settlement by Europeans until long after contact had been made on the East and Gulf coasts, as well as in the Southwest (Denevan 1976).

Figures of 7,400-10,000 are assumed to be rather reliable estimates for the Cherokees' nadir population during the early to mid-eighteenth century (Goodwin 1977), and application of a 20:1 or 25:1 depopulation ratio indicates that the pre-contact population would have been between 150,000 and 250,000. The difference between these estimates and Kroeber's estimate of 22,000 is highly significant. A quarter of a million inhabitants would have had a larger impact on the region's physical landscape than a comparatively scant population of 22,000 people. Obviously, the likelihood of extensive forest clearance would have been much greater.

The aboriginal inhabitants had been important components in the region's ecosystem. When disease, a major perturbation, decreased their numbers or eliminated them from some areas entirely, a major ecological change took place. Geographer Erhard Rostlund (1960) determined that buffalo (*Bison bison*) had not entered the Southeast by A.D. 1500, but migrated into the region after the middle of the sixteenth century, extending their habitat to the Atlantic and Gulf coasts. Historian Alfred Crosby suggests that the dramatic decrease in numbers of Amerindians opened up an ecotone for the buffalo.

Something had kept these animals out of the expanses of parklike clearings in the forest that periodic Amerindian use of fire and hoe had created. That something declined or disappeared after 1540. That something was, in all likelihood, the Amerindians themselves, who naturally would have killed the buffalo for food and to protect their crops (Crosby 1986).

ABORIGINAL SETTLEMENT FEATURES AND THE USE OF FIRE

Topography was probably the determining factor in the distribution of Indian settlements (Dickens 1976). Virtually all sites occurred along relatively extensive floodplains. A nucleated village of two or three acres appears to have been the predominant type of settlement, although sites could have been as small as a quarter of an acre, or as large as six acres (Dickens 1976). Villages ranged in size from a few houses to perhaps as many as fifty houses surrounded by log palisades. Large areas of bottomland adjacent to the villages were probably maintained for agricultural activity (Dickens 1976). Fire was the principal tool used by Indians to clear vegetation. Despite frequent historical reference to fire, and the documentation of "Indian old fields," Indian use of fire in North America has been greatly underestimated (Brown 1948; Day 1953; Gersmehl 1970; Goodwin 1977; Johannessen and others 1971; Martin 1973a, 1973b; Maxwell 1910; Thompson and Smith 1970). Fire was useful in driving game and opening the forest "to increase visibility, improve forage, expose the mast, and help keep down the weeds" (Gersmehl 1970). In the Great Smoky Mountains, fires were set at frequent intervals to encourage the growth of certain plant species, such as blueberries (*Vaccinium vacillans*), which were useful for human consumption as well as wildlife habitat (Lindsay 1976).

The Cherokees, perhaps inadvertently, used fire for forest management. Plants having relatively little value, such as white pine, hemlock, birch, maple, and weeds were burned in order to encourage the growth of more valuable species. The Indians also burned the areas surrounding their villages to prevent catastrophic fires (Goodwin 1977).

Eastern Woodland Indians set fire periodically to burn accumulated litter and undergrowth and to encourage grassland (Thompson and Smith 1970). Periodic fire was especially important for the maintenance of prairies and canebrakes. Sondley has documented the existence of expansive grassland communities in the Asheville Basin at the dawn of white settlement.

Most of the lands on and near the French Broad River . . . were in prairies.... At the mouths of the smaller streams in that region tributary to the French Broad River were large canebrakes extending for miles up those tributaries (Sondley 1930).

Ralph Hughes determined that under continuous protection from fire, cane stands "lose vigor, thin out and die" (1966). Moreover, canebreak deterioration can be prevented with periodic fire. Thus, because canebreaks were present in the Asheville Basin at the onset of pioneer settlement and because their maintenance requires frequent fire, it seems likely that the Cherokees set fire to the Asheville Basin at regular intervals in order to clear the land of brush and trees. Following pioneer settlement, a combination of fire suppression (or a decrease in burning), uncontrolled grazing, and cultivation of floodplains was probably responsible for the decline of the extensive canebreaks.

Perhaps the most widespread use of fire by the Indians was in the preparation of land for agriculture. After undergrowth was burned, larger trees were killed by girdling. Planting began when sunlight passed through the dead branches; maize, beans, and squash were usually planted in the same field (Brown 1948). Maize (*Zea mays*) was the most important staple in the Indians' diet, and may have been cultivated as early as 100 B.C. It was planted extensively on the floodplains of major streams and rivers. Corn was harvested in the late summer and early fall and was often processed into several different items. These most often included various flours and cakes such as succotash, samp, hominy, hoe cake, and ash-cake. Corn was also a principal ingredient in soups and stews. Beans (*Phaseolus*), probably introduced at about 800 A.D., were next in importance as a cultivated crop, (Yarnell 1976) and were usually planted alongside corn. In fact, cornstalks were often used as beanpoles. The use of beans and corn in combination implied "complementation" in the natives' diet and as a result provided high nutrition. Squashes (*Cucurbitaceae*) including pumpkins, gourds, and summer crookneck, were also an important staple. Certain squash varieties had been cultivated as early as 2300 B.C. The Cherokees planted squashes beside beans and maize. The sunflower (*Helianthus annuus*) was probably domesticated during the second or third millennium B.C. (Yarnell 1976) and had a multitude of uses. For example, its seeds yielded an edible table oil and flour that could be made into bread (Goodwin 1977).

Some wild edibles, such as spinach-like pigweed (*Amaranthus*) and goosfoot (*Chenopodium album*), grew along wet ditches and streams. Blackberries (*Rubus argutus*), raspberries (*Rubus odoratus*), and blueberries (*Vaccinium vacillans*) were used. Nut-bearing trees provided the Indians with acorns, chestnuts, and walnuts, and sap from some trees provided sweetening agents such as maple syrup. Because Indians were strongly dependent on food from "wild" vegetation, some authorities believe that the Indians themselves were responsible for the wide distribution of certain trees, such as mockernut hickory (*Carya cordiformis*) and black walnut (*Juglans nigra*) (Goodwin 1977; Maxwell 1910).

The Cherokees obtained a number of fruits through contact with the Europeans in the sixteenth, seventeenth, and eighteenth centuries. These introduced fruits included watermelon (*Citrullus vulgaris*), peach (*Prunus persica*), apple (*Malus pumila*), and pear (*Pyrus communis*). Orchards were generally confined to moist, sandy soils at elevations below 3,000 feet; however, isolated stands of apple trees are at elevations up to 5,000 feet.

The Indians undoubtedly depended heavily on wild plants and animals for food, and they nurtured some forestland as a source of such foods. They also cleared large areas of settlements to provide fuelwood, and cleared extensive areas for agriculture.

Accounts of travelers document the abundance of cultivated fields and expansive grasslands throughout the Cherokee country. De Soto, in 1540, marched for a day through cultivated fields in southwestern North Carolina; subsequent explorers include De Luna in 1559-1561, Pardo in 1566-1568, Batt in 1667, Lederer in 1670, Needham and Arthur in 1673, Cuming in 1730, and Timberlake in 1762 (Boume 1904; Hudson and others 1985; Hudson 1987; Sondley 1977; Williams 1927, 1928). Perhaps Bartram's account of his travels of 1775 are the most informative. The botanist reported extensive open prairies and fields of corn along the Little Tennessee River Valley (Harper 1958).

Virtually all permanent native settlements were limited to the floodplains of major streams and rivers for good reason. Their economy was based principally on agriculture, and it was impractical, if not impossible, to farm on steeply sloping terrain or at high elevations where erosion and microclimatic conditions were unfavorable. In southwestern North Carolina, the 3,000-foot contour follows the boundary between lands that are relatively suitable for agriculture and those that are not; the same is likely true for much of the southern Appalachians. Slopes are typically gentle below 3,000 feet and are typically much steeper at higher elevations.

Indians used fire to clear land for agriculture, and it is likely that some fires burned larger areas than intended. On shallow soils serotinous needleleaf conifers tended to dominate following a burn. On deep soils and open slopes hardwoods persisted or invaded after a fire. Deep-soiled, sheltered mesic sites were probably less susceptible to burning.

Rostlund suggested that in the pre-contact southeastern United States, the aboriginal inhabitants' burning of vegetation resulted in maximum land clearance. After their depopulation and the concomitant reduction in frequent burning, the area of cleared land decreased and the proportion of forestland increased (Rostlund 1957). Silvical characteristics of some forested areas in the southern Appalachians seem to support

Rostlund's hypothesis. For example, in the contemporary Joyce Kilmer Memorial Forest in southwestern North Carolina, a high proportion of old-growth yellow-poplar dominates some mesic sites. Yellow-poplar is an aggressive pioneer species on fertile sites following drastic disturbance (McCracken 1978), and in examining the forest, Lorimer has determined that "disturbances as far back as 1550 are almost certainly indicated by substantial numbers of the intolerant tulip tree in corresponding age classes" (Lorimer 1980). Possibly a fifteenth- to sixteenth-century Indian settlement that was located at sites now dominated by yellow-poplar (*Liriodendron tulipifera*) was a source of major disturbance. Perhaps after the European introduction and the subsequent diffusion of epidemic disease during the mid-fifteenth century, the settlement was largely depopulated, and pioneer species, such as yellow-poplar, invaded previously cleared areas.

CONCLUSION

The ability of aboriginal inhabitants to clear forest has often been grossly underestimated. In fact, anthropogenic perturbations over the last one or two millennia have accounted for much of the Southeast's forest composition, which is dominated by disturbance-initiated species (Buckner 1989). In the southern Appalachians, the Indians' livelihood depended on the use of fire to clear land and on the cultivation of crops along the floodplains of major rivers and their tributaries. Before contact with Europeans, the Cherokees and their ancestors probably cleared all bottomland in the region at one time or another. Moreover, the Cherokees' pre-Columbian ancestors may at one time have been numerous enough to clear all land below the 3,000-foot contour.

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